Unveiling hybridization-driven speciation: Insights from the genomic evolution of *Xiphophorus*

[1] Camelia Oroian, [2] Adela Maria Dăescu

[1] Faculty of Horticulture and Business in Rural Development, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania; [2] Department of Cell Biology, Histology and Embryology, Faculty of Veterinary Medicine, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania. Corresponding author: A. M. Dăescu, adela.daescu@yahoo.com

Abstract. This article critically examines the groundbreaking findings of Du et al (2024) on the evolutionary genomics of the genus *Xiphophorus*. By sequencing and annotating the genomes of all 26 known species and three undescribed taxa, the study sheds light on the evolutionary history and hybridization events that have shaped the genetic, phenotypic, and ecological diversity of these freshwater fishes. The research demonstrates that hybridization often precedes speciation, with extensive genomic admixture influencing traits such as melanoma susceptibility and puberty timing, critical to reproductive isolation. Furthermore, the study explores gene family expansions, hybrid genome stabilization, and their roles in speciation processes. These findings challenge traditional views of speciation and underscore the importance of hybridization in driving genetic novelty and adaptation. This work solidifies *Xiphophorus* as a model genus for evolutionary, genomic, and biomedical research, with implications for conservation biology and human disease studies.

Key Words: *Xiphophorus*, hybridization, speciation, melanoma, reproductive isolation, phylogenomics, biodiversity, genome stabilization, evolutionary biology.

The purpose of this article is to critically examine and highlight the findings of the study conducted by Du et al (2024) on the evolutionary genomics of the genus *Xiphophorus*. This analysis focuses on their investigation into the evolutionary history, hybridization-driven speciation, and the genetic underpinnings of traits such as melanoma susceptibility and puberty timing. By presenting the implications of these discoveries, this article aims to contextualize their significance within the broader fields of evolutionary biology, genomics, and conservation science, offering insights into how hybridization and genetic novelty drive biodiversity and contribute to our understanding of complex biological processes.

An interesting study was conducted by a team of researchers including Kang Du, Juliana Morena Bonita Ricci, Yuan Lu, Mateo Garcia-Olazabal, Ronald B. Walter, Wesley C. Warren, Tristram O. Dodge, Molly Schumer, Hyun Park, Axel Meyer, and Manfred Schartl, who represent institutions such as Texas State University, Stanford University, the University of Konstanz, Korea University, and the University of Würzburg. Their expertise spans multiple disciplines, including evolutionary biology, phylogenomics, and molecular genetics. Du et al (2024) aimed to understand the evolutionary history of the genus *Xiphophorus*, a group of freshwater fishes commonly known as swordtails and platyfishes (Petrescu-Mag 2007; Miller et al 2010). This included sequencing and annotating the genomes of all 26 known species and three undescribed taxa to generate a comprehensive genomic resource. They sought to resolve phylogenetic uncertainties and investigate the role of hybridization in speciation, focusing on how these events have shaped genetic, phenotypic, and ecological traits (Du et al 2024). Another key objective was to study the molecular evolution of genes linked to cancer, such as melanoma, and those affecting puberty timing, which are involved in reproductive isolation (Liu et al 2020). Additionally, the team examined changes in gene family size, hybrid ancestry, and genome stabilization after hybridization events (Du et al 2024).

The researchers achieved several important results. They successfully assembled high-quality genomes for all *Xiphophorus species* and constructed phylogenetic trees using mitochondrial and nuclear data, which clarified evolutionary relationships within the genus (Du et al 2024). These analyses revealed significant discordance between mitochondrial and nuclear phylogenies (Figure 1), indicative of extensive hybridization events during the genus's evolutionary history. Hybridization was shown to frequently precede speciation, as evidenced by the hybrid ancestry in Southern swordtail species like *Xiphophorus clemenciae* Álvarez, 1959 and *Xiphophorus monticolus* Kallman, Walter, Morizot & Kazianis, 2004, which contained more than 10% hybrid-derived nuclear genomic content from ancestral platyfish lineages (Du et al 2024). This study also identified significant changes in gene family sizes, including expansions in olfactory receptors, melanocortin 4 receptors, and genes associated with cancer (see also Lu et al 2023). The xmrk oncogene, which induces melanoma in certain hybrid lineages (Weis & Schartl 1998; Petrescu-Mag & Proorocu 2022), was found to have originated in the Northern swordtail and platyfish clades, although it has been independently lost in some species (Du et al 2024). Furthermore, the timing of male sexual maturity was linked to defective copies of the mc4r gene in certain species, which influenced traits like body size, courtship behavior, and dominance, contributing to prezygotic reproductive isolation (Du et al 2024; see also Liu et al 2019). The study also demonstrated how hybrid genomes stabilize after hybridization through recombination, with hybrid-derived regions showing distinct patterns of divergence and substitution rates, which likely facilitated the speciation process.

The findings of Du et al (2024) are significant for several reasons. By demonstrating that hybridization often precedes speciation, the research challenges traditional linear views of speciation and highlights the importance of genetic admixture in generating evolutionary diversity. The discovery of genes linked to melanoma and puberty timing in *Xiphophorus* (see also Liu et al 2020) provides valuable insights into the genetic basis of these traits, with potential applications in cancer research and the study of metabolic regulation in humans (Du et al 2024). The results also contribute to broader discussions in evolutionary biology about the role of hybridization as a mechanism for adaptation and genetic novelty, particularly in vertebrates. The comprehensive genomic resources generated in this study solidify *Xiphophorus* as a powerful model for research in evolutionary biology, genetics, and biomedical sciences (Schartl & Walter 2016; Schartl & Lu 2024). Additionally, the understanding of hybridization and speciation processes (Schumer et al 2013; Petrescu-Mag 2018; Petrescu-Mag & Popa 2018) in these fishes has implications for their conservation, especially in light of environmental changes and habitat loss (Păsărin & Petrescu-Mag 2011; Petrescu-Mag et al 2013). This study underscores the complex interplay between hybridization, genome evolution, and speciation, providing a detailed framework for studying these processes in other organisms.

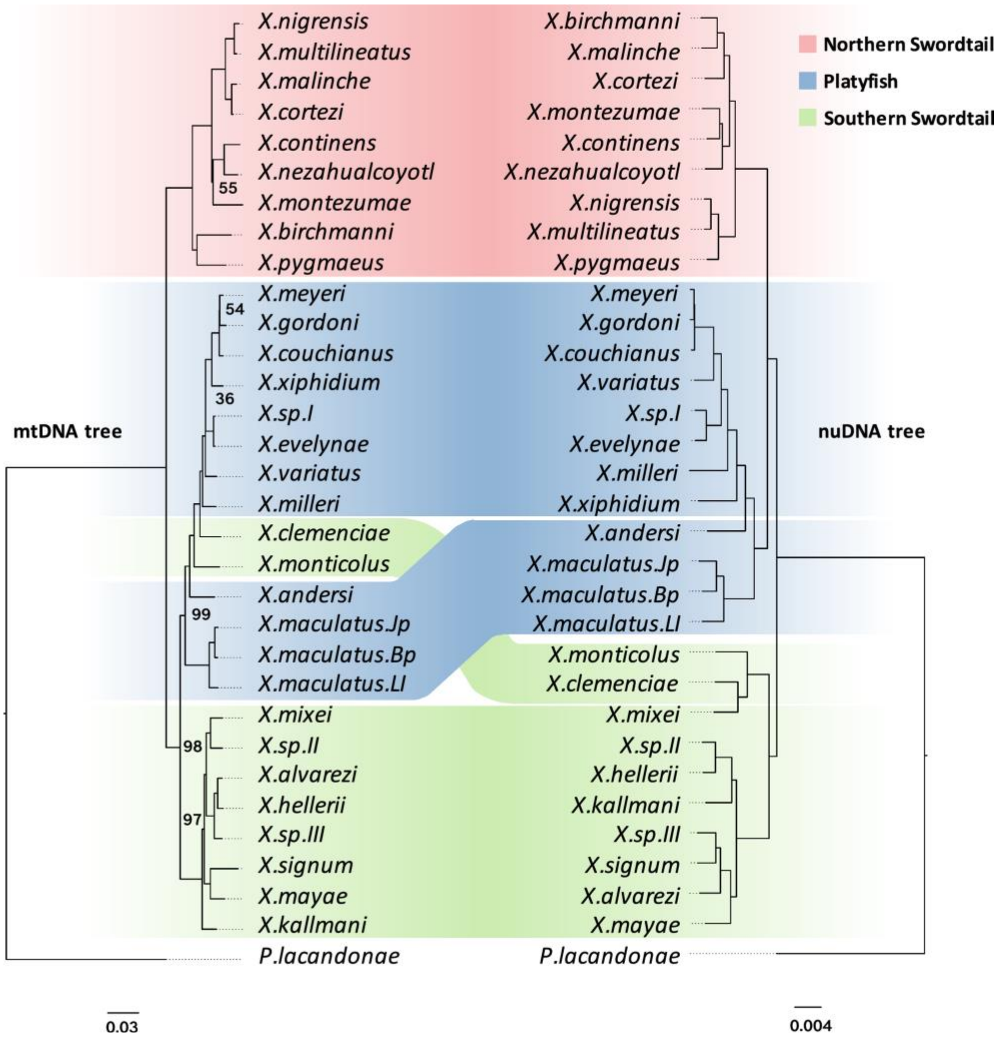

Figure 1. Phylogenetic trees were constructed using a maximum-likelihood method for the mitochondrial genome (~15 kb, left) and nuclear genome sequences (~342 Mb, right). Numbers on the nodes represent bootstrap support values; nodes without numbers means that they are 100% supported (source: Du et al 2024).

References

Du K., Ricci J. M. B., Lu Y., Garcia-Olazabal M., Walter R. B., Warren W. C., et al, 2024 Phylogenomic analyses of all species of swordtail fishes (genus *Xiphophorus*) show that hybridization preceded speciation. Nature Communications 15:6609.

Liu R., Kinoshita M., Adolfi M. C., Schartl M., 2019 Analysis of the role of the Mc4r system in development. growth, puberty medaka. Front Endocrinol 10:213.

Liu R., Du K., Ormanns J., Adolfi M. C., Schartl M., 2020 Melanocortin 4 receptor signaling and puberty onset regulation in *Xiphophorus swordtails*. Gen Comp Endocrinol 295:113521.

Lu Y., Rice E., Du K., Kneitz S., Naville M., Dechaud C., et al, 2023 High resolution genomes of multiple *Xiphophorus* species provide new insights into microevolution, hybrid incompatibility, and epistasis. Genome Research 33(4):557-571.

Miller E. G., Karlslake E. B., Masanoff J. R., Park J. P., Sammons A. J., Watson L. C., Newaj-Fyzul A., Petrescu-Mag I. V., Breden F., Allen T. C., Bourne G. R., 2010 Poeciliid livebearing fish polymorphisms: providing answers to questions of color, sex, mate acquisition, and personality. In: G.R. Bourne and C.M. Bourne (eds), The CEIBA Reader: an introduction to the people, ecosystems, plants, animals and cuisine of CEIBA Biological Center, Guyana. St. Louis, MO, Yerfdog Publishing. Chapter 4.21.

Păsărin B., Petrescu-Mag I. V., 2011 What we expect from Poeciliids for the future in terms of evolution. Poec Res 1(1):24-26.

Petrescu-Mag I. V., 2007 [Ecology of poeciliid fishes and the importance of their research]. In: [Applied Ecology]. Petrescu-Mag I.V. (ed.), 303-319.

Petrescu-Mag I. V., 2018 An evolutionary approach to homosexual behavior in Poeciliid fishes. Poec Res 8(1):24-26.

Petrescu-Mag I. V., Popa N., 2018 Ornamental varieties of the Xiphophorus genus: taxonomy is obsolete and powerless. Poec Res 8(1):13-14.

Petrescu-Mag I. V., Proorocu M., 2022 Melanoma in Poeciliid fishes: the trade-off between beauty and cancer. Poec Res 12(1):17-22.

Petrescu-Mag R. M., Păsărin B., Şonea C. G., Petrescu-Mag I. V., 2013 Customer preferences and trends for aquarium fish in Transylvania (Romania). North-West J Zool 9(1):166-171.

Schartl M., Lu Y., 2024 Validity of *Xiphophorus* fish as models for human disease. Dis Model Mech 17: dmm050382.

Schartl M., Walter R. B., 2016 *Xiphophorus* and Medaka cancer models. Adv Exp Med Biol 916:531–552.

Schumer M., Cui R., Boussau B., Walter R., Rosenthal G., Andolfatto P., 2013 An evaluation of the hybrid speciation hypothesis for *Xiphophorus clemenciae* based on whole genome sequences. Evolution 67(4):1155-1168.

Weis S., Schartl M., 1998 The macromelanophore locus and the melanoma oncogene Xmrk are separate genetic entities in the genome of *Xiphophorus*. Genetics 149:1909-1920.

Received: 15 November 2024. Accepted: 26 December 2024. Published online: 30 December 2024.

Authors:
Camelia Oroian, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Horticulture and Business in Rural Development, 3-5 Calea Manastur, 400372 Cluj-Napoca, Romania, e-mail: camelia.oroian@usamvcluj.ro
Adela Maria Dăescu, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Veterinary Medicine, Department of Cell Biology, Histology and Embryology, 3-5 Calea Mănăştur Street, 400372 Cluj-Napoca, Romania, e-mail: adela.daescu@yahoo.com

How to cite this article:
Oroian C., Dăescu A. M., 2024 Unveiling hybridization-driven speciation: Insights from the genomic evolution of *Xiphophorus*. Poec Res 14(1):20-23.