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Early Molecular Sex Determination before Gonadal Differentiation in Russian Sturgeon (*Acipenser gueldenstaedtii*): Mechanisms and Recent Advances

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Abstract

This mini-review synthesizes recent research on the molecular mechanisms governing sex determination in the Russian sturgeon. The paper highlights that while morphological sex differentiation is extremely delayed, genetic and epigenetic cues establish sexual fate much earlier. The authors present a model where a female heterogametic (ZW) system, marked by the *AgSDY* gene, initiates transcriptional programs (*dmrt*1 vs. *foxl*2) that are then stabilized by epigenetic modifications, providing a molecular basis for early sexing long before gonadal changes are visible.

Keywords

Sex Determination, Sturgeon, *Acipenser gueldenstaedtii*, AgSDY, *dmrt*1, *foxl*2, Gonadal Differentiation, Epigenetics, Sex-Linked Markers, Early Sexing

1. Introduction

Sex determination is a fundamental biological process that governs the development of gonads and secondary sexual characteristics in vertebrates (Figure 1). In fish, sex determination systems are remarkably diverse, ranging from genetic sex determination (GSD) to environmental sex determination (ESD), and in many species, complex interactions between the two mechanisms exist [1] [2]. Unlike model teleosts such as zebrafish (*Danio rerio*) or medaka (*Oryzias latipes*), which exhibit clearly defined master sex-determining genes (e.g., *dmrt*1*bY*, *gsdfY*, or *sdY*), ancient lineages such as sturgeons (family *Acipenseridae*) possess large, polyploid genomes and slow developmental processes that obscure early sex differentiation. The Russian sturgeon (*Acipenser gueldenstaedtii*) represents a key model among sturgeons for both evolutionary and applied research. This species displays an exceptionally delayed onset of gonadal differentiation, often not occurring until 5 - 7 years post-hatching [3]. Polyploidy can "blur single-gene readouts" because polyploid genomes typically contain multiple copies of many genes (paralogs), which often share similar sequences and partially overlapping functions. Consequently, the expression signal of a putative sex-determining gene may actually represent the combined activity of several paralogous loci rather than a single regulatory switch. This redundancy makes it difficult to identify a unique master sex-determining gene based solely on individual gene expression patterns. For this reason, an axis-level analysis—considering coordinated regulation across the hypothalamus-pituitary-gonadal axis—is required to resolve the true architecture of primary sex determination. Consequently, sex cannot be reliably identified morphologically or histologically during the juvenile phase, presenting a significant challenge for both developmental biology studies and aquaculture practices. Traditionally, sex identification required invasive biopsy or ultrasound examination at advanced ages. These approaches are costly, stressful to the fish, and inefficient for large-scale breeding programs. Over the last decade, technological advances in genome sequencing, transcriptomics, and epigenomics have begun to unravel the genetic basis of sex determination in *Acipenser* species [4]-[6]. Evidence from genomic mapping suggests that sturgeons likely follow a female heterogametic ZW system, as identified in *A. ruthenus* [4], and possibly conserved in *A. gueldenstaedtii*. Importantly, the discovery of a sex-linked marker, AgSDY, homologous to the salmonid *sdY* gene, has enabled early molecular sexing even before gonadal differentiation [5]. Moreover, transcriptomic analyses revealed early, sex-biased expression of genes such as *dmrt*1, *sox*9, *amh*, and *foxl*2, long before structural gonad formation is detectable [7]. Beyond the identification of genetic markers, emerging data suggest that epigenetic regulation—including DNA methylation and [8] gene promoters, such as *cyp*19*a*1*a* and *foxl*2 [8] [9]. These findings support the hypothesis that sex determination in sturgeons may involve both genetic and epigenetic factors, operating well before visible gonadal differentiation. The purpose of this review is to synthesize current knowledge on molecular mechanisms of sex determination before gonadal differentiation in Russian sturgeon. We focus on recent advances from genomic, transcriptomic, and epigenetic research that contribute to understanding the early molecular cues defining sexual fate in this ancient lineage. By integrating these findings, we aim to outline a framework for future developmental and molecular studies on sturgeon sex differentiation. In aquaculture, non-molecular methods allow the separation of males and females only after approximately 3 - 4 years, when gonadal differentiation becomes morphologically detectable. In contrast, molecular approaches that identify sex-specific genetic markers enable this process to be carried out much earlier—

only a few months after hatching—greatly improving the efficiency of stock management and production.

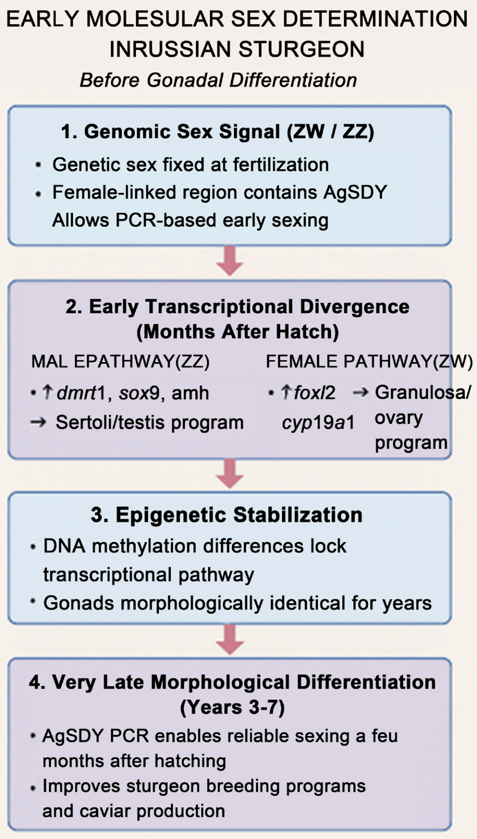

Figure 1. Early molecular sex determination in Russian sturgeon.

2. Sex Determination before Gonadal Differentiation

Sex determination in Russian sturgeon (*Acipenser gueldenstaedtii*) occurs long before gonads become histologically distinguishable. Like other members of Acipenseridae, this species shows an unusually long undifferentiated gonadal phase, making it difficult to study sexual fate based solely on morphology [10] [11]. However, recent advances in molecular biology have revealed that sex-specific regulatory mechanisms are already active during early development—well before visible gonad differentiation.

2.1. Timing of Early Gonadal Development

The primordial gonad in sturgeon embryos originates from paired genital ridges that form alongside the mesonephros during early juvenile development [12]. In *A. gueldenstaedtii*, the gonadal primordium appears at approximately 8 - 10 weeks post-hatch, consisting of undifferentiated germ cells surrounded by somatic precursors (Hurvitz *et al.*, 2007). However, no histological signs of testis or ovary differentiation are detectable until at least 3 - 4 years of age, and full ovarian follicular organization is not observed until 5 - 7 years [10].

In Russian sturgeon (*Acipenser gueldenstaedtii*), the gonad primordium forms early, but morphological sex differentiation is markedly delayed—typically years after hatching—so classic histology cannot resolve sex in juveniles [3] [10] [13]. This temporal gap makes "pre-gonadal" sex determination a molecular question: do sex-biasing cues arise before clear ovarian/testicular architecture? Evidence from congeners and closely related sturgeons indicates that genetic signals (putative ZW system) are present from fertilization, implying that sex fate is specified well before histological dimorphism [4]. In *A. gueldenstaedtii*, the AgSDY sex-associated region is detectable in fin or blood DNA of juveniles, supporting an early, constitutionally encoded signal [5].

2.2. Histological Observations: What We Can (and Can't) See Early

Juvenile gonads in sturgeon appear as undifferentiated paired ridges with germline stem cells surrounded by somatic precursors; no reliable ovarian or testicular cords are evident during early life stages. Markers like oocyte nests, cortical alveoli, or testicular lobulation emerge much later, often years into rearing [10] [13]. Consequently, biopsy/ultrasound methods are either inconclusive or deferred to advanced ages, reinforcing the need for molecular readouts prior to morphology.

2.3. Early Molecular Events and Candidate Pathways

Multiple lines of evidence suggest sex-biased molecular priming precedes visible differentiation:

> Genetic signal: The *AgSDY* marker segregates with sex in Russian sturgeon and can be PCR-detected in juveniles, analogous (though not identical) to the salmonid master sex gene *sdY* [5] [14].Gonadal pathway genes: Early transcriptional biases are reported for testis-pathway genes (*dmrt*1, *sox*9, *amh*) and ovary-pathway genes (*foxl*2, *cyp*19*a*1*a*) before overt histology, suggesting pre-differentiation priming of Sertoli-/granulosa-like programs [6] [15]. Epigenetic regulation: DNA methylation and putative chromatin remodeling around *cyp*19*a*1*a* and *foxl*2 promoters show sex-biased patterns in sturgeon and other fishes, consistent with epigenetic gating of early sex trade [9]. These marks are plausible upstream or parallel modulators that canalize gene expression prior to tissue-level differentiation.

2.4. Working Model

A parsimonious model is that a constitutional genetic cue (ZW/ZZ + AgSDY-linked region) sets initial sex fate; transcriptional programs (e.g., *dmrt*1/*sox*9/*amh* vs *foxl*2/*cyp*19*a*1*a*) begin to diverge in undifferentiated gonad primordia; and epigenetic modifiers stabilize these programs until the much-later histological manifestation (**Table 1**).

Table 1. Timeline: histology vs. molecular readouts (conceptual).

Dimension	Very early (embryo/larva)	Juvenile (months-years)	Visible differentiation (years)
Histology	Gonad ridge forms; no dimorphism	Still largely undifferentiated; biopsy inconclusive	Ovarian/testicular structures evident
Genetic	ZW/ZZ state fixed at fertilization	**AgSDY** PCR sexing feasible (juveniles)	—
Transcriptome	Subtle bias begins in sex genes?*	**Sex-biased expression** of *dmrt*1/*sox*9/*amh* vs *foxl*2/*cyp*19*a*1*a* detectable by RNA-seq/qPCR	Strongly dimorphic
Epigenetic	Establishment of marks begins	**Promoter methylation differences** at *cyp*19*a*1*a*/*foxl*2 measurable	Consolidated patterns

*Inferences based on early sampling in sturgeon cohorts and comparative teleost data [6] [15].

2.5. Methodological Notes for "Pre-Gonadal" Inference

Because classic histology lags far behind, sampling design is critical: 1) nonlethal DNA (fin clip) for AgSDY PCR sexing [5]; 2) small gonad primordium punches (when feasible) or surrogate tissues for RNA-seq/qPCR of sex genes (Khodadoust and Amiri, 2023); and 3) bisulfite sequencing or targeted methylation assays for epigenetic marks [9] [16]. Longitudinal designs that track the same individuals from juvenile stages to first visible differentiation provide the strongest evidence for pre-gonadal molecular divergence.

3. Molecular Pathways and Candidate Genes

(*Elsevier style · Author-Year; research focus: mechanisms prior to histological differentiation*)

3.1. Testis Axis: dmrt1 → sox9 → amh (Sertoli/Testis Program)

Across vertebrates, *dmrt*1 is a pivotal male-pathway regulator that maintains testis identity and represses ovarian genes; in fishes it often sits upstream of *sox*9 and *amh* [15]. In sturgeons, juvenile and pre-differentiated cohorts show male-biased transcription of dmrt1 (sometimes multiple paralogs due to polyploidy), with coordinated elevation of sox9 and amh, consistent with Sertoli lineage priming before overt cord formation [6] [15]. Functionally, amh is expected to suppress pro-ovarian aromatase and support testis morphogenesis, a relationship inferred from expression anti-correlations with cyp19a1a in early sturgeon gonads and from conserved teleost models [15].

Key points (testis axis):

dmrt1 upregulation appears early (juveniles), preceding histological dimorphism [6] [15]. sox9 co-bias suggests Sertoli differentiation potential in undifferentiated primordia [15]. amh elevation aligns with repression of the aromatase pathway (Devlin and [15]).

3.2. Ovary Axis: foxl2 ↔ cyp19a1a (Aromatase) (Granulosa/Ovary Program)

The canonical pro-ovary module in fishes comprises foxl2 and cyp19a1a; FOXL2 transactivates the cyp19a1a promoter to raise estrogen synthesis and stabilize ovarian fate [1]. In sturgeons, foxl2 and cyp19a1a show female-biased expression during and before visible ovarian differentiation, indicating pre-gonadal commitment of granulosa-like programs [15]. Recent transcriptome work in *Acipenser dabryanus* further suggests foxl2 may also regulate hsd17b1, extending its role beyond aromatase maintenance to broader steroidogenic control [17].

Key points (ovary axis):

foxl2/cyp19a1a bias can be detected before ovarian histology, marking an early ovary trajectory [17] [18]. Feedback with male genes is antagonistic: dmrt1/sox9 tend to repress cyp19a1a, while foxl2/estrogens counter-repress dmrt1 [1] [19]. Epigenetic gating (promoter methylation/chromatin) of cyp19a1a and foxl2 has been reported in fishes and indicated in sturgeon datasets, consistent with early pathway stabilization prior to morphology [8] [9].

3.3. Cross-Talk, Redundancy, and Polyploidy

Sturgeons' ancient polyploid genomes mean candidate genes may exist as paralog families with partitioned or redundant functions [4] [20]. This can blur single-gene readouts (e.g., multiple dmrt1 or sox9 copies), yet axis-level signals (combined male-pathway vs. ovary-pathway expression) remain informative. Integrating ZW genetics—notably the female-specific region described by [4]—with these axis signatures supports a working model in which a constitutional ZW/ZZ cue biases early transcriptional programs and epigenetic mechanisms consolidate them until late histology.

3.4. Practical Molecular Readouts (Pre-Gonadal Stage)

For Russian sturgeon and congeners, several assays now target these axes before gonadal differentiation:

Axis expression panels (qPCR/RNA-seq): *dmrt*1, *sox*9, *amh* vs. *foxl*2, *cyp*19*a*1*a* in juvenile primordia or minimally invasive tissue [6] [15]. Female-specific DNA markers (ZW-linked): the female-specific region discovered by [4] underpins cross-species markers (e.g., SSM4/) validated in several *Acipenser* spp., including Russian sturgeon cohorts [17]. These PCR assays provide pre-gonadal sex calls, which can be combined with axis expression to strengthen inference. Epigenetic assays: targeted bisulfite or reduced-representation approaches at cyp19a1a/foxl2 promoters to detect early sex-biased methylation as an additional layer of evidence [9].

4. Conclusions

Early sex determination in Russian sturgeon is controlled by a multilayered interplay of genetic, transcriptional, and epigenetic mechanisms that precede visible gonadal differentiation by several years. Although the species lacks external sexual dimorphism and exhibits one of the latest gonad differentiation timelines among vertebrates, recent genomic and transcriptomic advances have revealed that sexual fate is established long before histological markers appear. The identification of the AgSDY sex-linked region provides the first reliable DNA-based tool for early sexing, while early sex-biased expression of key regulatory genes—such as dmrt1, sox9, and amh in presumptive males, and foxl2 and cyp19a1a in presumptive females—demonstrates early divergence of testis- and ovary-associated pathways. Epigenetic signals, including DNA methylation of sex-related gene promoters, further consolidate these early trajectories and likely help stabilize sex fate in a polyploid genome.

Together, these findings support a model in which a constitutional ZW/ZZ genetic signal initiates sex determination, transcriptional programs diverge during juvenile development, and epigenetic modifications reinforce the pathway well before morphological differentiation. For aquaculture, this knowledge offers a foundation for developing early noninvasive sexing technologies that can dramatically improve caviar production efficiency and resource management. From an evolutionary perspective, Russian sturgeon provides a unique window into ancestral mechanisms of vertebrate sex determination. Continued integration of genomic, transcriptomic, and epigenomic data will be essential for fully resolving the molecular sequence of events that govern sexual development in this ancient lineage.

Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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