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Opinion

The Genetic Feasibility of Gonadal Development and Fertility in Polyodon-Acipenserid Interfamilial Hybrids: An Opinion on the Chromosomal Basis

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Abstract

Interfamilial hybridization between American paddlefish (*Polyodon spathula*) and Acipenserid (sturgeon) species produces viable hybrid offspring. However, the potential fertility of these hybrids is a critical issue for understanding sex determination mechanisms within Acipenseriformes, as well as for aquaculture and species conservation programs. Investigating the fertility of such hybrids requires an integrative focus on the genetic basis of sex determination and gonadal differentiation. Based on current knowledge of sturgeon sex determination systems, the fundamental genetic framework for gonadal development is assumed to be at least partially retained in Polyodon–Acipenserid hybrids. Nevertheless, the meiotic processes governing gametogenesis may be affected by chromosomal or regulatory incompatibilities. To date, the available evidence does not indicate complete disruption of meiosis. However, further cytogenetic and molecular analyses are needed to clarify the extent of functional gametogenesis and the reproductive potential of these hybrids.

Keywords: interfamilial hybridization; Acipenseriformes; sex determination mechanism; chromosomes

1. Introduction

Hybridization is a key driver of speciation [1,2] and a major creative force in evolution [3,4]. It plays a larger role in evolution than previously recognized [5] and occurs more readily in fish than in other vertebrates [6]. Within fish, it is more common in polyploid species, as these species are more tolerant of foreign genomes than non-polyploid species, thus favoring hybridization events [7–9].

The polyploid status of a species can be autopolyploid in origin, where the chromosome number is duplicated within a species, or allopolyploid in origin, where polyploidization occurs due to the hybridization of genomes from different species [1]. In autopolyploid species, the duplicated chromosomes are intraspecific and homologous. In allopolyploid species, hybridization by genome duplication results in homologous sets of chromosomes consisting of homologous chromosomes from the original (purebred) genomes [10]. In the Acipenseriformes order, several polyploidization events of allopolyploid origin have occurred during the evolution of Acipenseridae, whereas in the Polyodontidae family, polyploidization is known to be of autopolyploid origin [11].

Polyploid speciation is when the chromosome number of the hybrid progeny doubles. If it remains diploid (i.e., without chromosome doubling), it is called homoploid hybrid speciation [1]. Although polyploid hybrids are genetically distinct from their parent species, they often exhibit impaired gametogenesis and reduced gamete formation. This reduction is often associated with imperfect chromosome pairing [1].

2. Artificial Hybridization of American Paddlefish (*Polyodon spathula*; Family Polyodontidae) With Acipenserid (Sturgeon) Species (Family Acipenseridae)

The crossing of different purebred sturgeon species to produce interspecific hybrids, in addition the research programs, is also justified in aquaculture production. The main reason is to exploit heterosis (e.g., higher growth or survival rate and feed utilization), which could lead to increased yields in sturgeon aquaculture products.

Successful hybridization of the American paddlefish with sturgeon species was recently described in three species crossing combinations [12–14]. A common feature of all three hybridization combinations is that viable progenies were produced when the American paddlefish served as the paternal species and the sturgeon species as the maternal parent. In hybrids resulting from the cross between

American paddlefish and sterlet (*Acipenser ruthenus*), the hybridization was unidirectional. In other words, crosses between male American paddlefish with female sterlet produced viable progenies, whereas hybrid zygotes produced in the reciprocal crosses died in the late blastula or early morula stage [14]. This may be due to asymmetric gamete compatibility and mitochondrial inheritance biases. Two of the three American paddlefish (120 chromosomes [6]) crossed with sturgeons of ~120 chromosomes [6] (American paddlefish × sterlet, and American paddlefish × pallid sturgeon [*Scaphirhynchus albus*]) produced hybrid progeny with the same chromosome number as American paddlefish [13,14]. In contrast, hybridization between American paddlefish and Russian sturgeon (*Acipenser gueldenstaedtii*, ~250 chromosomes [6]) resulted in two hybrid groups with different chromosome numbers. The chromosome number for offspring derived from the cross between American paddlefish and sterlet was identical to the parent species (~120) [14], while the hybridization between American paddlefish and Russian sturgeon produced mainly triploid (3n; chromosome number ~180) and pentaploid (5n; chromosome number ~300) hybrid groups. However, aneuploidy and genetic mosaicism (1n/3n; 1n/5n) have also been observed in the somatic cell lines of some hybrid progenies [12], but the reasons of these chromosomal aberrations were not assessed.

The sexual development and fertilization potential of hybrid individuals have so far been studied only in American paddlefish and Russian sturgeon hybrids. Hybrids also with smaller and larger genome sizes included both genetically male and female individuals. Notably, some male hybrids showed gonadal development with the presence of spermatogonia cells [15]. This shows a similar pattern of sexual development to that described for interspecific hybrids of sturgeon species with different chromosome numbers [15].

3. Chromosomal Basis of the Sex Determination System in the Acipenseriformes Order

The polyploid status of paddlefish and sturgeon species is the result of whole genome duplication (WGD) events, although the details are still unclear. According to some authors, a WGD event occurred in the common ancestor of paddlefish and sturgeons approximately 200 million years ago, followed by lineage-specific rediploidization in sturgeons. Consequently, although paddlefish and sturgeons retain some shared gene duplications, their genome shows a mosaic pattern comprising both shared and lineage-specific duplicated regions [16]. In contrast, some researchers have hypothesized that an independent autopolyploid (polyploidization within species) paddlefish WGD event and multiple sturgeon WGD events in Chinese sturgeon (*Acipenser sinensis*) and sterlet species resulted from autopolyploidization processes [17]. All chromosomes from American paddlefish and sterlet, but especially the six macrochromosomes, were found to have high collinearity [17].

Genome duplication events in sterlet and American paddlefish were followed by asynchronous rediploidization, resulting in a complex mosaic of diploid and tetraploid chromosome segments in the genomic architecture [18,19]. As such, these species can be considered to represent an intermediate state between paleotetraploidy and diploidy. In the case of American paddlefish, numerous chromosomal rearrangements occurred before and after the WGD event [20]. These rearrangements involved the fusion of macrochromosomes and fission of microchromosomes (dot-like chromosomes) [20], phenomena that have also been observed in sterlet. Based on these findings, it was proposed that large macrochromosomes in the Acipenseriformes order were formed by the fusion of ancient chromosomes, while microchromosomes were formed by the fission of single chromosomes [20]. Thus, chromosomal fusions and fissions appear to be an integral part of the evolutionary history of Acipenseriformes species.

A comparison of the chromosomes of sterlet and American paddlefish reveals a high (although not complete) degree of homology, with a high degree of similarity in chromosome size, shape, and gene sequence. The macro- and microchromosomes are highly conserved in individual chromosome segments [20], indicating the slow evolutionary rate of sturgeons.

If chromosomes from the American paddlefish and various sturgeon species undergo bivalent pairing during meiosis, this indicates meiotic stability [16], which is likely to result in normal gametogenesis and therefore fertility. In contrast, multivalent pairing would suggest meiotic instability [16], which is more likely to lead to abnormal gametogenesis and infertility.

The chromosome number in hybrids resulting from crosses between American paddlefish and sterlet is approximately the same as that of the parental species (~120) [14]. However, hybridization between American paddlefish and Russian sturgeon can also result in hybrid groups with triploid (3n, ~180) and pentaploid (5n, ~300) chromosome numbers, and cases of aneuploidy and genetic mosaicism have also been observed among the hybrid progeny [12].

Inter-species crosses between Acipenserid species with the same ploidy are known to be fertile, whereas crosses between parent species with different ploidy result in sterile, aneuploid, or semi-fertile (sterile females, males with limited fertility) hybrid progenies [21]. Recent genomic studies have identified the chromosomal region responsible for sex determination in these species [22,23]. Based on genetic marker analyses derived from this region, along with earlier studies involving mainly gynogenetic approaches, it is now accepted that both sturgeons and American paddlefish have a female heterogametic (ZZ-ZW) sex determination system [24–26]. A 180-million-year-old female-specific genomic region has been identified in sterlet and Russian sturgeon. This region appears to have been retained even after additional WGD events [22]. The sex chromosomes in sturgeons are homomorphic, and are thought to contain an extensive pseudoautosomal region that is capable of recombination [22].

Studies of gynogenetic and triploid white sturgeon (*Acipenser transmontanus*) and bester (*Huso huso* female × *Acipenser ruthenus* male) found a 1/6 male (ZZZ) and 5/6 female ratio, consisting of 4/6 ZZW and 1/6 ZWW female genotypes. This distribution suggests a high frequency of recombination between the centromere and the sex-determining region [24,27,28]. Ruan *et al.* [23] reported that a female-specific marker developed from six Amur sturgeon (*Acipenser schrenckii*) individuals failed to determine the sex of American paddlefish, but successfully identified the sex of sterlet and Russian sturgeon. This indicates that family-specific differences in female-specific DNA sequences exist between Polyodon and Acipenser. In the case of male American paddlefish and female sterlet or Russian sturgeon hybrids, one or more W chromosome(s) can only be of Acipenser origin. This makes it possible to detect the W chromosome(s) in paddlefish–sturgeon hybrids and thereby determine the genetic sex (female) of hybrid individuals [15]. In male hybrids, Z chromosomes are inherited from both parental species (paternal and maternal), and in some cases, these Z chromosomes can support spermatogonial development [15].

In addition to these genes, other sex differentiation genes have also been identified [29]. A complex polygenic sex determination system has been hypothesized. However, this contradicts the identified sex-determining chromosomal region and sex-specific genomic markers identified and confirmed in many Acipenseridae species [22,23].

4. Reproductive Performance of Interfamilial Hybrids in Acipenseriformes

The first level of reproductive performance concerns hybrid sterility, with the main cause being disturbances between homologous parental chromosomes (abnormal conjugation or non-disjunction) during meiosis [30]. However, a contrasting viewpoint suggests that hybrid sterility cannot be attributed solely to chromosomal incompatibilities, but may instead result from genetic incompatibility (lack or improper interaction or regulation of gene products from different genomes) or the combined effects of chromosomal and genetic factors [31]. If the sex-determining genes in the hybrids are incompatible, this plays a greater role in the development of sterility than chromosomal incompatibility (e.g., different chromosome types). The organism is able to compensate for chromosomal incompatibility through mechanisms such as Robertsonian and tandem fusions, inversions, insertions, duplications, and amplifications [31], as demonstrated by the high frequency of chromosome number and type variability in sturgeon hybrids.

For example, the chromosomes of American paddlefish and sterlet exhibit a high, although not complete rate of homology [20]. This is similar to the chromosomes of sterlet and beluga (*Huso huso*), in which the hybrids (sterlet × beluga) are also capable of producing fertile gametes [27]. The pachytene checkpoint mechanism plays an important role in hybrid sterility. It is a meiotic surveillance system that prevents the formation of genetically and chromosomally defective gametes [32]. This mechanism is presumably absent in sturgeon species [33].

There is no clear evidence of complete genetic incompatibility in viable hybrids between sterlet or Russian sturgeon and American paddlefish, despite the fact that the two parental species exhibit distinct anatomical and physiological characteristics that are genetically determined. In both American paddlefish and sturgeon species, the gene losses following WGDs may be compensated by their capacity for (possibly spontaneous) autopolyploidization [34]. For instance, female-specific DNA sequences have been successfully identified in hybrids between American paddlefish and Russian sturgeon [15]. Current evidence also suggests that gonadal development may proceed to the formation of spermatogonia in some male hybrid individuals [15].

5. Conclusions

In hybrids of American paddlefish and sterlet, the same chromosome numbers and presumably bivalent chromosome pairing (resulting in stable meiotic processes), together with the absence of the pachytene checkpoint mechanism in Acipenserid species, may determine potential fertility in both sexes.

In contrast, in hybrids of American paddlefish and Russian sturgeon, which involve parental species with different ploidy levels, it is more likely that multivalent chromosome pairing occurs. This is reflected by the increased genomic instability observed in such hybrids, including aneuploidy and genetic mosaicism, which are characteristic consequences of abnormal chromosome segregation.

These observations suggest that partial fertility for American paddlefish × sterlet hybrids may be possible in both sexes, whereas American paddlefish × Russian sturgeon hybrids are likely to exhibit semi-fertility or sterility.

The gonad development and fertility of American paddlefish × pallid sturgeon hybrids have not yet been investigated. This is an important issue because the pallid sturgeon belongs to a different genus than the sterlet and Russian sturgeon. Such research could thus further elucidate the genetic basis of sex development mechanisms in Acipenseriformes species.

Author Contributions

JK conceptualization and writing original draft; GK, KB designed the study; BK and EV provided help and advice on the interpretation of data and search references; EV finally and language editing. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript. All authors have participated sufficiently in the work and agreed to be accountable for all aspects of the work.

Ethics Approval and Consent to Participate

Not applicable.

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Conflict of Interest

The authors declare no conflict of interest.

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