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Vertebrate sex-determining genes play musical chairs

Les gènes qui déterminent le sexe des vertébrés jouent aux chaises musicales

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ARTICLE INFO

Article history:

Received 18 March 2016

Accepted after revision 26 April 2016

Available online xxx

Keywords:

Sex-determination

Evolution

Vertebrates

Fish

Next-generation sequencing

Mots clés :

Déterminisme du sexe

Évolution

Vertébrés

Poissons

Séquençage nouvelle génération

ABSTRACT

Sexual reproduction is one of the most highly conserved processes in evolution. However, the genetic and cellular mechanisms making the decision of whether the undifferentiated gonad of animal embryos develops either towards male or female are manifold and quite diverse. In vertebrates, sex-determining mechanisms range from environmental to simple or complex genetic mechanisms and different mechanisms have evolved repeatedly and independently. In species with simple genetic sex-determination, master sex-determining genes lying on sex chromosomes drive the gonadal differentiation process by switching on a developmental program, which ultimately leads to testicular or ovarian differentiation. So far, very few sex-determining genes have been identified in vertebrates and apart from mammals and birds, these genes are apparently not conserved over a larger number of related orders, families, genera, or even species. To fill this knowledge gap and to better explore genetic sex-determination, we propose a strategy (RAD-Sex) that makes use of next-generation sequencing technology to identify genetic markers that define sex-specific segments of the male or female genome.

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R É S U M É

La reproduction sexuée est une des fonctions biologiques les plus conservées au cours de l'évolution. Cependant, les mécanismes génétiques et cellulaires qui gouvernent la différenciation d'une gonade embryonnaire indifférenciée vers le sexe mâle (testicules) ou femelle (ovaires) sont très variables. Les déterminismes du sexe ont évolué à plusieurs reprises et de façon indépendante dans les différents groupes de vertébrés, et ils sont, soit contrôlés par l'environnement, soit basés sur des systèmes génétiques plus ou moins

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<http://dx.doi.org/10.1016/j.crv.2016.05.010>

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Please cite this article in press as: Q. Pan, et al., Vertebrate sex-determining genes play musical chairs, C. R. Biologies (2016), <http://dx.doi.org/10.1016/j.crv.2016.05.010>

complexes. Chez les espèces qui possèdent des systèmes génétiques simples de détermination du sexe, les déterminants majeurs du sexe localisés sur les chromosomes sexuels vont enclencher le processus de différenciation des gonades, qui conduira in fine à la différenciation de testicules ou d'ovaires. Jusqu'à présent, très peu de gènes déterminants majeurs du sexe ont été identifiés chez les vertébrés et, en dehors des mammifères et des oiseaux, ces gènes ne sont apparemment pas conservés en dehors de groupes taxonomiques restreints, voire même au sein de la même espèce. Pour combler ce peu de connaissances et pour obtenir une vision plus large de l'évolution de ces déterminants majeurs du sexe, nous proposons une stratégie (RAD-Sex) basée sur l'utilisation d'une technologie de séquençage moderne pour identifier, chez de nombreuses espèces, des marqueurs génétiques associés au sexe mâle ou femelle.

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1. Introduction

Sex has been termed the “queen of problems in evolutionary biology”, and how sex is determined in the animal kingdom has always been a major question with “debates on the origin of the sexes that took place long before the beginning of the scientific era” [1]. Indeed, since the beginning of this “scientific era”, important knowledge has been acquired on this topic with, for instance within the quite recent “genetics era”, the important discovery of sex chromosomes, followed by the identification of the master gene governing the acquisition of the male sex in human and in mouse [2]. Despite huge efforts in the last decades, however, our knowledge of master genes controlling genetic sex-determination has remained limited [3]. The relative scarcity of information on sex-determination (*SD*) genes is mainly due to major scientific and technical barriers that hinder the precise identification of these *SD* genes in many species. Classical approaches for the characterization of *SD* genes have always relied on the intimate knowledge of a group of specialists working on very few species. Their success has often been guided either by educated guess and candidate gene approaches [4,5], or by tedious searches for sex-linked markers with various time-consuming methods [6–9]. The relatively few species investigated now with regards to *SD* genes have been selected based on practical interests (for instance species easy to maintain in captivity [8–12]) or economical (for instance important aquaculture species [5,13–15]) and these species always had preexisting genetic and/or genomic information available. There is then an urgent need to address the question of the evolution of *SD* genes using a large-scale, unbiased approach that would not rely on or need such previous knowledge.

2. A glimpse into sex-determination and *SD* genes evolution in vertebrates with a focus on fish species

The field of evolution of sex-determination and *SD* genes in vertebrates has long been shaped by knowledge gathered in mammals, because previously this was the only group for which the master *SD* gene, *SRY*, was known [2]. The generally accepted hypothesis for the mechanism by which an *SD* gene can evolve, namely by allelic diversification of an autosomal gene towards a male or

female sex-promoting function, and subsequent maintenance of the male-specifying allele as a male dominant *SD* gene on the proto-Y chromosome, was satisfied by *SRY* and its supposed progenitor *SOX3* [3]. In 1999, *dmrt1* was found as a candidate gene for *SD* in chicken, which proposed a different mechanism, namely dosage sensitivity [16]. In 2002, the first fish *SD* gene was identified in the medaka, *Oryzias latipes*. Unexpectedly, this gene, called *dmrt1bY* or *dmy* [7,10], arose by a gene duplication event from the autosomal *dmrt1a* gene being transposed to the proto-Y, adding another evolutionary mechanism for the emergence of an *SD* gene. Full sequencing of the male-specific region of the Y chromosome (MSY), the first to be known after the human Y, revealed that several additional predictions of the general theory of Y chromosome evolution were also not fulfilled, like stepwise diversification on an autosome, recombination suppression, degeneration of Y-linked genes, and accumulation of male-favoring genes [17]. This finding raised doubts about a unifying concept for the evolution of *SD* genes and heterogametic sex chromosomes.

Fish are uniquely suited to study the evolution of sex-determination and *SD* genes (Fig. 1). Comprising about half of the 60,000 species of vertebrates, fish show also the greatest variety of sex-determination. Unisexuality, simultaneous and consecutive hermaphroditism, environmental, and genetic sex-determination are found in different, often closely related species and the distribution of various mechanisms follows no obvious phylogenetic pattern. With respect to genetic *SD*, it became quickly clear after its first discovery that *dmrt1bY* of medaka is not the master *SD* gene of fish in general [14]. Despite huge efforts over more than a decade, *SD* genes of only a few more species have been added to this list, and all those species have strong monogenic sex-determination. In a sister species to medaka, *O. luzonensis*, and also in sablefish, *Anoplopoma fimbria*, allelic variations of a TGF β member gene named *gsdf*^Y determines male development [8,13]. In *Takifugu rubripes* (pufferfish) as well, allelic variation at a single nucleotide position of the *amh-receptor 2* gene, again a downstream component of the *SD* cascade in other vertebrates, controls phenotypic sex [6]. In the Patagonian pejerrey, *Odontesthes hatcheri*, a Y-linked duplicate of the *amh* gene drives male sex-determination [5], a situation that mirrors the evolutionary scenario of the medaka *SD*

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