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Sensing Non-sense in Animal Sex From Perspective of Transposable Elements

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ABSTRACT

Evolution of vertebrate species took shape through millions of years, where sex played an important role in maintenance of a lineage, genetic diversifications and reproductive isolation. On due course of sexual evolution, sex determination strategies have been proposed to flow from temperature dependent sex determination to genetic sex determination, which has been demonstrated as XY system in mammals and ZW system in birds. In contrary to this established conception, different lineages showed to have overlapping sex determining strategies. While searching possible reasons for these phenomenons, researchers observed that gene content of sex chromosomes is highly variable as far as their location and prevalence is concerned, which otherwise suggested autosomal origin of sex chromosomes. Although the exact mechanisms of gene transfer and thereby origin of sex chromosomes are yet to be unveiled, but chromosomal rearrangement and introgression has been hypothesized to be the possible effector. Transposable elements (TEs) are long been considered to be 'Selfish' or 'Junk' DNA material as most of the non-coding genomic regions are comprised by TEs, which did not make any sense to be a part of species genome. But recently, TEs are being considered to be a nature's tool for biological innovation by creating new regulatory elements, new coding sequences, genetic disruption and chromosomal remodelling. So, this has been postulated that TEs could facilitate rearrangement and introgression, which ultimately lead to evolution of sex chromosomes and sex determining genes through positive selection. Prevalence of highly repetitive sequences in sex chromosomes, particularly in Y, makes it a hot bed for TEs mediated rearrangement and introgression. In this review, I tried to discuss whether it makes any sense to focus on the role of TEs in sexual evolution of animals.

Introduction

Sex and sex chromosomes is the one of the greatest domain of biological research as this is the gateway for speciation through evolution. New species comes into existence through evolution, when a particular lineage diverts into reproductively isolated groups of organisms (Coyne and Orr, 2004). Although, different studies were carried out to

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analyse the process of reproductive isolation (Dobzhansky, 1937; Darwin, 1859; Coyne and Orr, 1989; Coyne and Orr, 1997; Abbott et al., 2013), and evolution (Dobzhansky, 1937; Darwin, 1859; Liou and Price, 1994; Rundle and Nosil, 2005; Maan and Seehausen, 2011; Seehausen et al., 2014;), but we are yet to reach a consensus regarding mechanisms of speciation. Small changes in genome through mutations and rearrangements accumulate over millions of years. These genomic changes encounter enormous selective force of nature. When time tested beneficial changes accumulate and propagate to next generations, a new species comes into existence. Sex chromosomes play a pivotal role in speciation as propagation of beneficial genomic changes to successive generations must pass through reproductive gateway. Thus, studies on animal reproduction may unveil multiple dimensions of genomic organisation, genetic pathways and mechanisms of genetic diversifications that lead to speciation through evolution.

Chromosomal rearrangements are considered to be one of the major sources of genetic variations and gene flow between species (Rieseberg, 2001; Kirkpatrick and Barton, 2006; Ayala et al., 2013; Baack et al., 2015). In this regard, role of transposable elements (TEs) in origination of new chromosomal rearrangements has been assessed in numerous studies (Lim, 1988; Ladeveze et al., 1998; Li et al., 2017). Until the late 1940s, genes were considered as orderly arranged stable, static entities on chromosomes (Morgan, 1922). In 1950, Barbara McClintock proposed dynamic nature of some genetic elements for the first time. She discovered a particular location on Maize chromosome 9, which breaks with an unusual high frequency. This dissociation (Ds) locus (that's how she termed it) can change its position within the chromosome (Transposition). She also discovered that the Ds element takes help from another locus, termed as activator (Ac), for this change its location event. The Ac locus is autonomous in nature and can change its position by its own. This very mobility of As and Ds elements within genome could lead to insertional mutagenesis and functions of already mutated gene can be restored by remobilization of the TEs (McClintock, 1950). Later, Ac was identified as an autonomous DNA transposon, which helps Ds, a non-autonomous transposable element for their transposition events. Ac encodes a transposase enzyme, which is responsible for transposition of the Ac transposon into a different location of the maize genome. Being a non-autonomous TEs, Ds lacks a functional transposase, so, depends on the Ac encoded transposase (Fedoroff, 1989).

Majority of the noncoding part of the genome, i.e. 'Junk', Selfish or non –sense DNA, as we named it, is made up of TEs. 80% of plant, 3–20% of fungal and 3–52% in metazoan (animals) genomic DNA are consisted of TEs (Wicker et al., 2007; Gregory et al., 2007; Bennetzen and Wang, 2014). According to their mode of transposition, transposons are classified into two groups, i.e. Class – I and Class – II. Class – I transposons, transpose themselves through RNA intermediate, whereas Class – II TEs transpose themselves through cut-and-paste mechanism by directly integrating the transposon DNA from former location to new genomic location. That's why Class – II transposons are also known as 'Jumping genes'. TEs insertion in new genomic location, either can disrupt existing coding or regulatory sequences, which can be deleterious to the species concerned (Okamoto and Hirochika, 2001; Feschotte et al., 2002; Woodhouse et al., 2006; Feschotte, 2008; Oliver and Greene, 2009) or may lead to beneficial changes by changing regulatory sequences, generating new coding sequences, generating new chromosomal variants, facilitating chromosomal inversions, or genomic expansions. TE borne mutations could be rapid (van de Lagemaat et al., 2003; Flutre et al., 2011; Kapusta et al., 2013). This has also been postulated that TEs are maintained ubiquitously pan–species through multilevel selection (Vinogradov, 2004; Fablet and Vieira, 2011; Brunet and Doolittle, 2015) as they have potentials to provide novel genetic and phenotypic traits upon which selection can act (Arkhipova and Meselson, 2005; Hollister and Gaut, 2009). Although, the role of TEs in speciation has been broadly unexplored (Werren, 2011), but considering evidential observations, this is high time to enquire whether transposable elements are at all non-sense?

Exception is rule of nature

As far as sex strategy is concerned, vertebrates follow two different sex determining strategies i.e. environmental sex determination (ESD) and genetic sex determination (GSD). ESD is also termed as temperature dependent sex determination (TSD). In marine turtles, alligators (Charnov and Bull, 1977), and even in some other reptiles (Sarre et al., 2004) eggs are being hatched to males or females depending either upon the environmental temperature or temperature of egg incubation. Mammals, birds, amphibians and many reptiles follow GSD, where sexes in these animals are being determined genetically. Mammals are having XY system, where males are having XY sex chromosomes and females are having XX sex chromosomes. Whereas birds and reptiles carry ZW system, where males carry ZZ sex chromosomes and females carry ZW sex chromosomes. In mammals, males carry heterogamety (XY), which is quite opposite to birds and reptiles, where females carry heterogamety (ZW). Both the systems share some similarity, e.g. in both the systems sex specific chromosome i.e. Y and W usually smaller in size and carry less number of active genes than X and Z chromosomes. Interestingly, there are exceptions where both the strategies overlap, e.g. there are a number of species where they follow GSD but devoid of any obvious sex chromosomes. Sex-determining genes are present on cryptic sex chromosomes (Ezaz et al., 2005). Particularly in reptiles, elements of both the ESD and GSD overlap (Quinn et al., 2007). In spite of having X and Y sex chromosomes, marine turtles strictly follow TSD, whereas in Lizards, either TSD or GSD or both can coexist in the same genus. Even against the traditional concept of sex determining strategies, lizards may possess any of the XY, ZW or TSD systems (Shetty et al., 1999; Matsubara et al., 2006).

Exceptions are available in autosomes of higher vertebrates as well. Platypus could be considered as an extraordinary mammal, as its genomic features show amalgamations of mammalian and reptilian characteristics. Platypus genome is small, like reptile genome and possesses fewer noncoding RNAs than higher mammals (therian genome, e.g. Human, Mouse, etc.). This phenomenon suggests that Platypus has evaded extensive retrotransposition, just like chicken (Warren et al., 2008). Bird genome, in general, is smaller than mammalian genome, and its gene rich microchromosomes contain few repetitive sequences. While comparison between closely related species e.g. human and chimpanzee (Hughes et al., 2005), enlighten us with recent changes in the hominid lineage, genome wide comparisons between most distantly related mammals, e.g. elephants and armadillos, marsupials etc. may provide us information regarding our common ancestry and how evolution shaped mammal-ness from a reptile-like ancestor. In the human genome, there are many conserved noncoding elements that arouse from TEs. These TEs inserted in eutherian lineage over a period of time through evolution. The major evolutionary innovation that occurred in eutherian genome was modification in the X chromosome (Mikkelsen et al., 2007).

During convergent evolution of species, adaptation in new environment and enabling invasion in new habitats has been proposed to be facilitated by TEs (Stapley et al., 2015). Encountering a new environment during adaptation in new habitat is often stressful. This is quite evident that stress and environmental challenges facilitate TEs mobilization across different taxonomic groups (McClintock, 1950; Tapia et al., 2005; Zeh et al., 2009; Comai et al., 2009). So, TEs dependent increase in genetic diversity could be observed when it's exactly needed (Casacuberta and Gonzalez, 2013; Belyayev, 2014).

Origins and evolution of sex chromosomes

Inter–species comparative gene mapping shows that X chromosomes consisted of a X conserved region (XCR) which is ancient in nature and present in all therian mammals, whereas X added region (XAR) got introduced in eutherian mammals more recently. For example, part of human X chromosome (long arm and pericentric region) is homologous to entire Marsupials X chromosome, and rest of the human X chromosome, represents an autosomal region in marsupials (Graves, 1995). When it comes to sex-specific element, i.e. mammalian Y or Birds W, they are considered to be highly variable region in the genome (Waters et al., 2001). Instead of these variability, sex chromosome pairs i.e. XY or ZW, retains certain homology, which is consistent with their autosomal homologues. For example human X and Y shares homology at pseudoautosomal region, which supports pairing and recombination during meiosis in males. Along with that, homology of most of the Y borne genes can be observed in X in its XAR, which suggests their derivation from X chromosome (Graves, 2006). This is long been proposed that sex chromosomes originated from autosomal chromosomes by gaining male determining role (Muller, 1964). Evolutionary evidences suggest that human chromosomes 9 and 5 share homology with chicken Z, whereas mammal X shares homology with chicken chromosome 4 and part of chromosome 1 (Nanda et al., 2000; Marshall and Shetty, 2000). Similar phenomenon could be observed between snake and bird species. For instance, chicken chromosome 2 shares homology with snake ZW, whereas snake chromosome 2 shares homology with bird ZW (Matsubara et al., 2006). Comparative study suggests that platypus sex chromosome is chicken alike rather than mammals (Watson et al., 1990; Veyrunes et al., 2008). Human Y chromosome borne *DAZ* and *CDY* genes, appear to be transposed from autosomes. This incidence suggests autosomal origin of human Y specific genes with functions in reproduction (Lahn and Page, 1997).

Present day molecular biology analytical tool strengthen us to analyse whole genome of any species. Genome analysis of rather non–model species like monotreme mammals, birds and reptiles suggests the origin of the therian XY sex chromosomes to be 210–180 million years ago. *SOX3* gene product considered to be involved in brain development in mammals, as its expression could be found mainly in the central nervous system (Collignon et al., 1996). Until recently, when cloning of marsupial *SRY* attempted, *SOX3* was discovered to be present in X chromosome (Foster and

Graves, 1994). *SOX3* gene play pivotal role in sexual differentiation of amphibians and reptiles and its expression could be observed in primordial germcell differentiation in fish (Yao et al., 2007) and gonadagenesis in chicken and X*enopus*. Interestingly, therian Y chromosome specific *SRY* gene is a derivative of *SOX3* gene. Interestingly, in platypus *SOX3* lies on autosome 6 (Koyano et al., 1997). These studies suggest origin of SRY could be correlated with *SOX3*. These evidences also support the theory of autosomal origin of sex chromosomes. Not only *SOX3*, but there are other such evidences, where several other male specific genes are having X homologues, which are having housekeeping or autosomal functions. For example, Y specific *RBMY* gene helps in spermatogenesis, whereas its X homologue *RBMX* involved in brain development (Tsend-Ayush et al., 2005). Similarly, X homologue of Y specific gonadoblastoma gene *TSPY*, is a candidate cell cycle gene (Delbridge et al., 2004). In some lineages, the expression of the Y specific genes like *SRY*, *RBMY* has been lost completely. Deletion or Degradation of chromosomal content of Y is quite evident throughout different mammalian species (Graves, 2006). For example, *UBE1* gene, which is responsible for spermatogenesis in mouse, could be found in mouse Y, whereas, in human *UBE1* has no copy on Y chromosome. Expression of *ATRX* gene could be found only in marsupial Y, but not in other therian group of animals (Pask et al., 2000). Similarly, mouse *ZFY* plays an essential role in spermatogenesis, whereas in human, *ZFY* is having housekeeping functions (Lahn and Page, 1999). Interestingly, some of species like mole vole (*Ellobius*) and Ryukyu spiny rat devoid of any Y chromosomes, so there is neither *SRY* nor *ZFY* genes present (Just et al., 1995; Sutou et al., 2001). In Ryukyu spiny rat, several other Y specific genes seem to be transferred to X chromosome (Arakawa et al., 2002). Although intensive studies are required to assess the proper mechanism of sex chromosome evolution, but this has long been hypothesized that sex chromosomes originated from autosomes when some of them gained sex determining functions. Once autosomal genes, gained or transformed to possess gender specific functions by evolutionary mecha-nism, which is yet unknown. As studies suggest that some of the therian species does not have any Y chromosome at all, it can be postulated that activity of Y specific genes in these lineages had been taken over either by X chromosomes or by any other autosome. Altogether, these evidences suggest sex chromosomes and their genes are pretty dynamic in nature as far as their evolution is concerned.

Transposable elements perspective

Chromosomal rearrangements are one of the major genetic factors which facilitate gene flow between species (Rieseberg, 2001; Kirkpatrick and Barton, 2006; Ayala et al., 2013; Baack et al., 2015), whereas, chromosomal inversions can preclude gene flow. Although active role of TEs in chromosomal rearrangements and inversion still needs to be addressed further (Lim, 1988; Ladeveze et al., 1998; Li et al., 2017), some indications suggest role of TEs in genetic introgression cannot be over ruled. In introgression, transfer of genetic material takes place through production of inter species fertile hybrids, which can be observed in nature, across all domains of life (Ellstrand, 2014; Soucy et al., 2015). TEs might facilitate or impede introgression process as a whole, but having insight of role of TEs and its relation with introgression may provide us crucial knowledge regarding the process of gene transfer within and between species and evolutionary mechanism of speciation. It could be hypothesized that genes and other genetic material could be exchanged within and between species either by TE mediated introgression or by transmission of TEs alone.

Although no systematic study has been conducted till now to assess the role of TEs in introgression, but some evidences suggest potential role of TEs in horizontal gene transfer (HGT) (de la Cruz and Davies, 2000; Thomas and Nielsen, 2005). For example, two species of beetles i.e. *Hypothenemus hampei* (Acuna et al., 2012) and the *Phaedon cochleariae*, acquired necessary genes to degrade plant cell walls for their diet through a HGT from bacteria (Pauchet and Heckel, 2013). Interestingly these acquired genes are flanked by two transposons in both cases. Similar events of introgression by TEs has been proposed for species pair of *Drosophila bifasciata* and *Drosophila imaii* (Haring et al., 1995), *Drosophila serido* and *Drosophila buzzatii* (Guerreiro, 2014), species of the willistoni groups (de Campos Bicudo,1973a; de Campos Bicudo, 1973b; Bock, 1978) and species of the simulans complex (Peccoud et al., 2017).

TEs mediated Introgression might also lead to the transfer across species boundaries [85, 86]. HGT acts as a bridge between diverged group of species during evolution (de la Cruz and Davies, 2000; Thomas and Nielsen, 2005). HGT is very common in Intra–species (Lucca Jr et al., 2014) and Inter–species. TEs mediated HGT could be anticipated between Drosophila and willistoni group of species. Considering the fact that these two groups diverged over 50 million years ago, hybridization between these two groups could be alleviated (Tamura et al., 2004). In multiple studies, inter-species HGT have been reported but the mechanisms of gene transfer amongst those species are yet to be ascertained (Vershinin et al., 2003; Schaack et al., 2010; Oliver et al., 2013) From all these evidences potential role TEs regarding introgression or gene transfer and thereby speciation through evolution remains suggestive but inconclusive.

Conclusion

Recent advancement in whole genome sequencing and thereby comparative genomics provides us new opportunities to unravel the complex mechanism of evolution of animal sex. On the course of evolutionary pathway, Sex chromosomes and sex determining genes of therian mammals, considered to be come into existence relative recently from the autosomes of other vertebrates. In spite of having shared sex-determining mechanism, bewildering variety of sex determination can be observed across the vertebrate species in terms of unrelated and/or overlapping mammalian XY, bird ZW and TSD. In mammals, along with meiotic activity, testis is considered to possess high mitotic activity and poor DNA repair mechanisms (Aitken and Graves, 2002). High degree of repetitive sequences is quite evident in mammalian sex chromosomes (Rozen et al., 2003). So, during each generation cycle in testis, sex chromosomes, particularly Y, is at potential risk of introgression through transposition (Aitken and Graves, 2002). In this manner, gene conversion in Y chromosomes could be possible by accumulated inverted repeats vis-à-vis TEs (Rozen et al., 2003). Creating new genetic regulatory elements and coding sequences, genetic disruptions, chromosomal remodelling are the most prominent tools by which TEs are being hypothesized to promote genomic differentiation within and between species (Zeh et al., 2009; Belyayev, 2014; Trizzino et al., 2017). Therefore, we should involve ourselves in explorative studies assessing role of TEs on such a domain, which is as variable and fascinating as sex. TEs have long been considered to be 'junk' or non-sense DNA material of species genome. Multiple studies have been carried out though in plant domain, assessing involvement of TEs in generating new genetic traits in species as far as evolution and adaptation are concerned. But, with the advancement of modern research, TEs must be a focus of research to assess whether these non-sense elements does make any sense in animal sex and its evolution or not.

Conflict of interest

None

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