NEW CODING SEQUENCES FORMATION BY VIRUSES WITH THE HELP OF HORIZONTAL TRANSFER AND GENE DUPLICATION

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Introduction

Horizontal transfer of genetic information is widely spread in prokaryotes, but previously it was rarely found in eukaryotes [1]. According to research that studied horizontal transfer in 26 animal species (10 species of primates, 12 fly species and 4 nematode species), the animals acquire tens and hundreds of genes in this way. Those genes are mainly coding for metabolic enzymes. Nematodes and Drosophila spp. still continue to acquire genes with the help of horizontal transfer. At the same time, the same research shows that only few genes acquired with the help of horizontal transfer. In the same time, there were only few genes found in humans and primates that were acquired with the help of horizontal transfer after their divergence from the common ancestor [2].

But the recently obtained reports concerning horizontal transfer events in humans allow to change this view and signify that the role of horizontal transfer in the vertebrate genome development is presently underestimated [3]. In course of the comparison between the human genome and the genomes of 53 vertebrate species 1467 genome regions, 2,5 M n. p. in total were found to be more similar to the non-vertebrate genome sequences than to the sequences of most vertebrate ones [3]. There are 642 genes located in those regions, and they were likely acquired through horizontal transfer.

According to the present data, mobile genetic elements are structures that regularly relocate between eukaryotic genomes [4]. In the database that contains all events of mobile elements, 2836 events of horizontal transfer were recorded in eukaryotes until October, 2017 [5].

Horizontal transfer is possible for all types of mobile elements [6-8]. As mobile elements are the main components of the nuclear genome of multicellular eukaryotes and are also important sources of genetic variation that catalyze the evolutionary novelties, the horizontal transfer of mobile elements can play a significant role in eukaryotic evolution.

Viruses are the suitable vectors for horizontal transfer of the genes and mobile elements, as they infect representatives of different taxonomic groups, are able to enter and exit the cell, can take up and transfer genetic material, including the host cellular RNA during the development if viral particles, and also are able to infect germ cells or their progenitors. Besides that, viruses retain genetic material outside the cell very well.

Horizontal transfer of genetic material by viruses

Despite the fact that there is little data concerning the spread of horizontal material by viruses, there is evidence of constant exchange of genetic material in some insects at least [9, 10]. Genome fragments and mobile elements of the butterflies Trichoplusia ni. are known to insert themselves into the genome of baculovirus multiple nucleopolyhedrovirus of Autographa californica (AcMNPV), that infects the T. ni. larvae. Every time when the AcMNPV virus infects the night butterfly T. ni, a significant quantity (from dozens to hundreds) and a great variety of DNA sequences of the moth genome integrate into the viral genome [10]**.** In average, 4.8% (from 1.1% to 14.3%) of the viral genomes in the AcMNPV population contain at least one fragment of cellular genome sequence.

Bakuloviruses are composed from double stranded DNA and also contain sequences from Hymenoptera and Diptera species as well. Most bakuloviruses are transferred in the form of so-called occlusive bodies (OB) that are in fact virions enclosed inside a protein matrix. OB bodies allow the virus to retain viability in the outside environment in course of several years. The formation of OB bodies allows the virus to infect the insects not as a single virion, but as a genetically polymorphic viral population.

A caterpillar that is orally infected with a dose of the virus that leads to the 50% mortality contains tens of thousands of OB. One OB contains approximately 100 virions, each one is composed of several AcMNPV genomes. Consequently, a caterpillar infected by thousands of AcMNPV genomes is more likely to be infected with a virus that carries foreign genetic material. Considering the fact that in average at least 4.8% bakuloviruses contain cellular genome sequences, and that the butterfly larva is usually infected with thousands of bakulovirus genomes, we can assume that every non-lethal infection can result in horizontal transfer of DNA.

Bakuloviruses can infect reproductive cells. Moreover, some individuals are quite resistant to the viral infection, which allows the foreign genetic material to integrate into the genome of germ cells and get transferred to the next generation.

It has been isolated 86 fragments of cellular genome integrated into the viral genome in course of the viral infection. 69 from the 86 sequences are mobile genetic elements that belong to 3 superfamilies of DNA transposons and to the 3 superfamilies of retrotransposons. We can conclude that DNA transposons predominantly integrate themselves into the viral genome, and they accomplish it with the help of the transposition mechanism. But besides the transposon DNA, other sequences also integrate into the genome. The mechanism of such integration is based on different types of recombination. In some cases, recombination depends on micro-homologic sequences sized from 1 to 20 n. p. The mechanism of integration of the cellular DNA points to the development of double strand breaks in the viral genome in course of its life cycle.

The sequences of the cell genome integrated into the various regions of the viral genome. All the 151 genes

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of the virus can be the targets for the host sequences integration. What was the most interesting, the pattern of integration of mobile elements into the genomes of Spodoptera exigua is similar to the pattern of integration into the T. ni genome. In other words, mobile elements of two different butterfly species predominantly integrated into the same regions of AcMNPV virus. Based on this evidence, it was proposed that the distribution of the integration sites for the butterfly genome fragments into the viral DNA is determined by the availability of the viral genome that in its turn is formed by the chromatin structure of the AcMNPV virus and its epigenetic modifications. A number of data obtained for the animal genomes shows that in fact the epigenetic modifications of histones and DNA determine for the most part the pattern of the mobile elements integration into the host cell genome. It seems that similar mechanisms form the availability for the integration of the cell genome into the genome of the virus.

Horizontal transfer of the transposon DNA through the AcMNPV virus is constant and recent transfer events can be found. At least for the 21 of 69 DNA transposons, integrated into the AcMNPV viruses, one or more events of horizontal transfer between T. ni and S. exigua from one side and one or two lineages from the other side was observed. The similarity of nucleotide sequences between DNA transposons of T. ni or S. exigua and DNA transposons of other insect species reaches up to 99%, which allows to suspect recent horizontal transfer events.

At the same time, in course of 10 infectious cycles, viral genomes lose all integrated fragments. In this way, multiple sequences of cellular genome integrate into the viruses in course of each infection cycle, but they are quickly lost by the population in the natural conditions.

Therefore, at least in some insects in their natural environment, viruses constantly perform horizontal transfer of the genes. The viral population is a gene reservoir, the content of which is constantly renewed and influences both the host organism evolution as well as, possibly, the evolution of viruses.

Giant double-stranded DNA viruses are horizontal transfer agents in vertebrates as well.

Giant DNA viruses of the mammals contain genes of cellular origin, therefore we can suppose horizontal transfer between viruses and animals can potentially take place. For instance, herpesviruses contain at least 20% bovine genes, i.e. this percentage of genes, present in all viruses of the family, has cellular origins, whereas other genes are acquired from viruses of other viral families [11, 12].

Mobile elements of the genome can insert themselves into the herpes virus genome. Teratorn-1-like viruses have evolved as a result of merge between a herpesvirus and piggyBac-like transposone that enabled the dissemination of herpesviruses in the genomes of bony fish [13]. It is quite likely that Teratorn-1-like viruses can use the transposase of the piggyBack element for the integration of the genome and distribution there, while the piggyBack trasnsposon acquires the ability for horizontal transfer between individuals and species with the herpesvirus help. The structure of the Teratorn-l-like element makes it an excellent vector for gene horizontal transfer.

Further studies have shown that piggyBac-like elements and Teratorn-1-like herpesviruses used to co-exist for a long time and their merging often takes place in the bony fish genomes [12].

Poxviruses, including the cattle papilloma virus (TATV), are represented by big DNA-containing viruses. TATV is related to the smallpox virus (VARV). Snake genome SINE mobile element inserted itself into the TATV virus with the help of retrotransposition [14] Based on these data, it was proposed that poxviruses can become vectors of horizontal transfer of SINE elements from reptiles to mammals.

Mobile elements, genome fragments and RNA molecules of the host genome can be packed into the viral capsids [15-17]. Single-stranded RNA viruses pack cellular RNA into the virions together with its viral genome [18].

Virus-like particles are spontaneously formed by FHV alfadanovirus that is composed of single strand RNA and omega virus NωV that belongs to tetravirus group and infects Nudaurelia capensis in the cellular line of Spodoptera frugiperda. Virus-like particles form in the case when only RNA that codes for the polypeptide precursor of capsid proteins is expressed in the cells of this line from the baculovirus vector [18]. Correspondingly, the particles do not contain RNA-dependent polymerase**.**

During the study of RNA contents of FHV and NωV – like particles it was found that virus-like particles contain predominantly ribosomal RNA and baculovirus vector transcripts, while 5,3 % of RNA, packed into the FHV-formed virus-like particles, are in fact mobile elements RNA of the cellular genome. Virus-like particles contain DNA transposons, as well as LTR and non-LTR retrotransposons. Virus-like particles formed by two viruses differ based on the number and type of packed mobile elements. FHV particles predominantly contain non-LTR R1 retrotransposon, while NωV – DNA transposon Mariner.

FHV virions also contain RNA molecules of the host cell origin and the latter compose approximately 1% of all packed RNA. Virions contain a significant part of mRNA, ribosomal RNA, non-coding RNA and mobile elements [18]. FHV viruses contain predominantly LTR retrotransposons. FHV and Nω virus-like particles differ considerably based on the assortment of included RNA molecules mRNA is usually packed into viruses, whole virus-like particles contain ribosomal RNA.

Therefore, viruses and virus-like particles do not just include cellular RNA into their contents; they form their own specific range of these molecules.

FHV viral particles contain endogenous retroviral components, as well as transcripts that code for reverse transcriptase, endonuclease and integrase. It is possible that with their help RNA, transported with the help of the particles, integrates into the cellular genome.

The ability of the viruses to pack cellular RNA molecules corroborates the idea of the existence of genetic

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information exchange mechanism between eukaryotic cells in nature.

Endogenous retroviruses and gene duplications in the host genome

Gene duplications are the source of genetic polymorphism and evolutionary changes [19]. Duplications allow t diversification of gene expression in specific cells and tissues on different development stages in response to different stimuli, and also lead to development of new functions and sub-functions of the genes themselves.

The sequencing of the mammalian genomes, including primates and rodents, has shown that approximately 90% of their genes did not undergo deletions, duplications or have become pseudo-genes from the moment of divergence from the common ancestor of mammals. The remaining 10% are objects of frequent duplications, deletions and pseudo-genes development [20-22]. These 10% belong to the gene families that are involved in the immune response development, toxin metabolism, are chemosensors or participate in procreation. Frequently, similar genes can be found in the genomes of different species.

As retrotransposons are homological sequences, their high concentration in the locus can lead to the destabilization and rebuilding of the latter. It is indeed shown that endogenous retroviruses can recombine with each other through non-allelic homological recombination (NAHR), and duplications, deletions and inversions can form as a result [23].

The murine genome region that codes for androgen-binding proteins (Abp) contains 64 paralogic genes. The Abp protein is a dimer that consists of alpha and beta-gamma subunits. The size of the region that contains the Abp genes is 3 million nucleotide pairs. It is located on the end of the 7 murine chromosome and contains 30 genes that code for the alpha subunit (Abpa), and 34 genes coding for the beta-gamma subunit (Abpbg).

The expansion of the family has occurred relatively recently and independently in mice and rats [24]. Moreover, even the murine lines differ in the quantity of the copies of the genes from this family [25].

How has exactly the gene amplification occurred and how has the family developed? Previously it was shown that two stages and two different mechanisms led to the gene expansion and development of 64 of the family genes in the murine genome [25]. In course of the first stage, the gene was duplicated together with the development of two daughter genes Abpa-Abpbg, located in two opposite directions. The pair of duplicated Abpa-Abpbg genes forms a module of further duplication. At the first stage, these duplications led to the formation of the blocks where all the modules were located in the inverse order. Most ancient amplifications of the locus were formed in this way. But at second stage, different blocks containing multiple genes were duplicated with the help of NAHR recombination and formed loci where blocks were arranged in a linear fashion.

Later, the researchers have obtained data that confirm the two-phase model of the family expansion and also proven the participation of the retrotransposons in the amplification of the Abp genes [26].

First, a high density of ERVII endogenous retroviruses and LINE1 retrotransposons in the Abp region of the genomes of rats and mice was shown, as well as pronounced decrease of their content in the boundary regions.

Second, while ERVII endogenous retroviruses are distributed approximately evenly between subfamilies that are species-specific and those that are common both for mice and rats, most LINE1 repeats remain species-specific. These data points to the probability that >50% of the ERVII endogenous retroviruses were inserted in the vicinity of the ancestor forms of Abp gene family, while LINE1 elements were almost completely absent in the Abp gene family region. Such distribution of the retrotransposons is a point in favor of two-phase model of the expansion of the gene family.

Third, a break point was found in the LINE1 retrotransposon that has caused the latest NAHR-promoted gene block duplication in the center of the Abp region in the genome of mice, which confirms the homological recombination between LINE1 elements as the mechanism of the second phase of Abp gene family expansion.

According to the modern views, duplications are the main source of new genes with new functions [19]. Duplications are usually followed by the duplicated genes divergence. Duplicated copies may acquire new functions, and in this case we are speaking about development of a new function, or can share the initial function that was performed by the ancestor variant between them. In the latter case, the process is called sub-functionalization. As a result of sub-functionalization, both genes become necessary for the performance of the function that was performed by the ancestor gene in the past.

It became possible to observe sub-functionalization during the study of the Abp gene family expansion. Abp paralogs, expressed in tear ducts and saliva ducts, were found in the ancestor lines of C57BL/6 mice. But in C57BL/6 mice, patterns of expressed genes of the Abp family in the tear duct and in the saliva duct do not cross over. The genes are highly expressed in both ducts in the ancestor form, but after duplication, expression of certain copies gets decreased in the saliva duct, while other copies are decreased in the tear ducts as a result of sub-functionalization [27].

Taking these data into account, it was proposed that at the first stages of the amplification process of the Abp gene family, an accumulation of the ERVII endogenous retroviruses took place in the locus [26], which in their turn formed new regulatory elements and reprogrammed gene transcription, which, in the end, led to sub-functionalization of the daughter gene modules [27]. This corresponds with the accumulation of the ERVII retroviruses in the genomes of rats and mice before the LINE elements appearance [26]. Line elements were inserted later and catalyzed the further amplification of the locus due to the homological recombination.

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But how common is the use of endogenous retroviruses and LINE retrotransposons in the murine and human genomes for the increase in the gene copies and creation of gene families? In order to answer this question, a study was performed that has elucidated the relationship between the content of endogenous retroviruses and LINE elements from one side and the size of the gene families from another [28]. The density of LINE and LTR elements around single genes is low, bit it increases with the increase in the gene family size.

A significant quantity of LTR elements overlap with the DNAse sensitive sites in the regions where small and big gene families are located. This confirms the role of LTR elements in the gene regulation and allows supposing that the insertion of the LTR elements plays a role in the sub-functionalization or neo-functionalization of the duplicated genes.

This way, the development of the gene families takes place in two phases. On the first phase of amplification, at least in a number of families, an increase of insertion of he endogenous retroviruses is observed and due to the LTR elements the regulatory network gets reformatted. During this neo-functionalization or subfunctionalization of duplicated genes takes place. After this, in the second phase, the process of increase in family gene copies continues due to the accumulation of the LINE elements that catalyze amplification. On this stage, the speed of endogenous retroviruses insertion decreases.

As LTR-containing retrotransposons and retroviruses code for the reverse transcriptase and endonuclease/integrase, and also are capable of replicative recombination, they can create gene retrocopies.

The LTR elements were known to be able to create gene retrocopies for a long time [29]. LTR retroelements flank the single genes in the corn genome [30], participate in the development of retrogenes in rice [31] and Arabidopsis [32].

But the fact that the existence of retrocopies of the genes formed by endogenous retroviruses is widespread was realized only after sequences that were shown to be gene retrocopies surrounded by LTR retrotransposons or retroviruses were found in the genomes of Drosophila, mammals, chickens, fish, mosquitoes, yeast and plants [33]. Retrocopies have evolved as a result of replicative recombination with the use of cellular RNA as a matrix during the shift in DNA synthesis that was performed by the reverse transcriptase. LTR sequences contain regulatory elements, so the retrogenes that have appeared as a result of such a process can be transcribed. In some cases, recombinants contained two or more genes of the host genome.

Conclusion

In conclusion, viruses cannot be viewed only as parasitic egoistical elements of the genome, but also as an instrument with the help of which the cellular genomes can acquire new genes, thus obtaining genetic information from other organisms and from the viruses themselves. Viruses are excellent vectors for genetic information transfer, as they can be well preserve outside the organism and can change hosts from time to time.

Besides the transfer of genetic information, the viruses function as a tool with the help of which the natural genetic engineering duplicates genes inside the host genome. It can be supposes that viruses are used much more widely as a tool for genome formation than is shown at present. For instance, endogenous retroviruses, activating inside the cell, can acquire parts of the nearby genes and transport them in other genome regions, containing other genes. In this way, new genes can appear in the genome of the cell.

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Besides the gene co-optation discusses in the previous article, viruses are able to form the cellular genome through horizontal gene transfer and by the copy number increase of the cellular genes with the help of amplification or retrocopies production. Previously horizontal transfer was thought to be a rare event. But genome sequence data for a wide range of organisms together with new analytical tools enable to detect a large number of horizontal gene transfer events across eukaryotes species. Many of these transfers have generated evolutionary novelties. Therefore it has been suggested that horizontal transfer of DNA may be an important evolutionary force shaping eukaryote genomes. However, the vectors involved in horizontal transfer of DNA between eukaryotes are poorly understood. Viruses have been proposed as candidate vectors for DNA transfer. Really they are transmitted horizontally, infect a variety of taxa, replicate inside host cells, some have a host genome integration stage and some viruses have germ cells tropism which allows transmission to the progeny. Despite these only limited but growing number of evidence argues that viruses could serve as horizontal transfer vectors between species. In this review we summarized these data. Many genes of large double-stranded DNA viruses have a cellular origin, suggesting the host-to-virus horizontal transfer of DNA. Indeed it has been identified a continuum influx of cabbage looper genetic material in baculoviruses genome. Furthermore at least 21 of the cabbage looper transposable elements integrated into baculoviruses genomes underwent repeated horizontal transfers between various insect species. These data identify potential recurrent gene flow both in virus-to-host and host-to-virus direction. Another example host RNAs encapsidation in the virions of single-strand RNA viruses. Gene duplication is a major driver of organism evolution. Gene retroposition is a mechanism of gene duplication whereby a gene's transcript is used as a template to generate retroposed gene copies. A genome-wide study across a fruit fly, mosquito, zebrafish, chicken, mouse, and human shows that LTR retrotransposons

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capable of creating retrocopies across a wide range of eukaryotes, which could subsequently evolve to be neofunctionalized retrogenes. Moreover it has been found a significant association between two retroviruses and lineage-specific gene family expansions in the human and mouse genomes. Altogether these data indicate that viruses, once considered as purely junk and selfish sequences, have repeatedly been used as a source of novel protein-coding genes during the evolution of eukaryote.

Keywords: endogenous retroviruses, horizontal transfer of genetic information, baculovirus, herpesvirus, alfanodaviruses, virus-like particles, gene duplication, gene retrocopies.

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