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Asking the Right Question about the Genetic Basis of Domestication: What is the Source of Genetic Diversity of Domesticated Species?

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Abstract

In this paper we investigate source of increased genetic diversity - one of the most obvious characteristics of domesticated species, leading to a wide range of phenotypic variability (breeds). The hypothesis that we put forward during the course of our studies focuses on transposons and retro-viral elements in the domesticated genomes. The inherent tolerance for transposition of mobile elements could lead to enhanced genetic diversity in the domesticated species.

Keywords Genetic diversity; Transposons; Glycolysis; Phenotypic

Introduction

For the last five years, the interest in genetic basis of domestication has been rising. Partially, this is due to the completion of sequencing of genomes of major domesticated mammals, which provided tools necessary for such an inquiry. Quite a few studies were published that looked for "domestication signature" within the domesticated genomes [1-4]. There has been launched an international consortium [5], whose main task is creation of a comprehensive catalogue of functional elements within domesticated genomes. It is anticipated, that exhaustive studies of genomic traces of artificial selection will broaden our understanding of how nucleotide sequences lead to phenotypic diversity.

A typical starting point of the search for the genetic basis of domestication is in defining features that clearly distinguish domesticated species from their wild relatives. The major phenotypic features of animal domestication were described in the mid-20th century. Clearly, for these phenotypic features there must exist corresponding genomic projections, which would include structural genes and also regulatory elements. Consequently, most of the research in this area focuses on differences between domesticated species and their wild relatives within specific gene sets [6]: for example, for pigs - within genes associated with feeding behavior [7], and dental changes [8]; for horses - in genes, which are responsible for lipid exchange, ion transport, muscle contraction, etc. [9,10]; for cattle - hornlessness, coat color, eye morphology, constitution, subcutaneous fat, ecological adaptation [11-13]. Is there a universal genetic feature of domestication? Despite extensive search, the only universal genetic feature of domestication found so far is the copy number increase of in the immune system genes and defensins [14-16].

D.K. Beliaev suggested to use the overall decrease in aggression towards humans as a selection target and a universal phenotypic feature of domestication. This idea was proven correct by the only domestication reconstruction experiment launched at that time - domestication of a wild fox. Generation after generation the least aggressive foxes were selected, leading to the appearance of typical domestication traits - dog-like tail shape, dog-like ears, dog-like barking type. Comparative analysis of gene expression revealed that hypothalamus-adrenal axis genes were involved in appearance of these dog-like features [17]. Other studies also demonstrated involvement in domestication of genes related to behavior, for example [18].

Comparative studies done by our group indicated that the universal features distinguishing domesticated animals from their closest wild relatives are 1) for the domesticated species - increased variability in metabolic enzymes of exogenous substrates; 2) for the closest wild relatives - increased variability in enzymes involved in energy metabolism (glycolysis, pentose phosphate pathway, Krebs cycle) [19]. Importantly, the degrees of variation between the two groups (domesticated vs. wild) were of the same order of magnitude. Moreover, in certain cases, genetic differentiation between breeds of domesticated species was higher than genetic differentiation between different wild species. This was an unexpected finding - the current view is such that increased inbreeding within domesticated compared to the wild animals should lead to decrease, not the increase in genetic variability. Other groups obtained results similar to ours [20]. The increase in phenotypic variability of domesticated species is, indeed, dramatic: number of different breeds, clearly distinguishable by phenotypic features for the 5 traditional agricultural species (goats, sheep, cattle, horses, pigs) is about 4500. This number of breeds is close to the estimated total number of all extant mammalian species [21].

Looking at all the accumulated data describing unprecedented phenotypic and genetic diversity of domesticated species, it becomes clear that the key to understanding the phenomenon of domestication is in finding the source of this diversity. It is worth to note, that despite multiple efforts throughout centuries to domesticate various species, only few species form the domesticated basis of agrarian civilization - cattle and sheep amongst animals; rice and wheat amongst plants. In his studies, Jared Diamond notes characteristics that disfavor domestication [22]. At the same time, we expect that there are also those characteristics and features that aid the domestication process. We suggest that these features should be linked to the higher level of

genetic variability. In turn, the higher level of genetic variability allows for interplay between natural and artificial selection yielding abundance in various phenotypic forms (breeds). This phenotypic, morphological variability within the same species is what so markedly distinguishes domesticated organisms from their closest wild relatives.

As already mentioned above, one of the few universal genomic features of domestication is the increase in copy numbers of the genes of immune systems and defensins - the antimicrobial defense system. It is known that the duplication of chromosomal segments, and also copy number variation of the short genomic regions are closely related to the mobility of retrotransposons [7]. Autonomous retrotransposons are mainly the descendants of exogenous retroviruses (of three classes), endogenous retroviruses, and the products of their intra-genomic evolution - long interspersed nuclear elements (LINEs), devoid of the long terminal repeats, but containing gene gag encoding a viral structural protein and also gene pol encoding a reverse transcriptase. Currently, there are available detailed databases of full-length endogenous retroviruses integrated into genomes of the major domesticated mammals [23]. There are also examples of the horizontal transfer of certain retrotransposons, whose presence relates genomes of otherwise taxonomically distant species [24-25]. There is ongoing discussion of importance of retrotransposon transfer in the evolution of vertebrates [26]. Structural and evolutionary connection between retrotransposons colonizing genomes of differ taxa becomes evident [27-29].

Previously, we demonstrated that in the genomes of domesticated plants and animals the frequency of short DNA fragments flanked by microsatellite repeats is higher compared to such frequency in the genomes of the closest wild relatives. Considering known connection between microsatellites and various mobile elements [30-32] allowed us to suggest relatively higher density of their mutual positions within genomes of domesticated compared to the wild relatives [19]. Consequently, we formulated the following hypothesis: the source of the higher genetic diversity of domesticated species (compared to the taxonomically related wild species) is the relatively higher degree of colonization of their genomes by transposable elements and the products of evolution thereof. In this article we further test this hypothesis by estimating frequencies DNA fragments flanked by long terminal repeats of retroviral origin within genomes of various domesticated animals and plants.

Materials and Methods

The population-genetic structure was studied by estimating polymorphisms of IRAP-PCR markers, which in turn were obtained by PCR using transposon-related long terminal repeats as primers. The following sequences were used for this purpose: the terminal region of retrotransposon SIRE-1, which constitutes 1/5th of the maize genome (GCAGTTATGCAAGTGGGATGAGCA) and belongs to the family of Pseudoviridae, members of which have env-like gene [33]; a region of the PawS 5 retrotransposon ((AACGAGGGGTTCGAGGCC), which belongs to the family of R173, members of this family are frequently associated with other retrotransposons within the genome of diploid rye [34]; a region of the barley retrotransposon BARE-1 (CCAACTAGAGGCTTGCTAGGGAC).

Also were used the following terminal retrotransposonal LTR of mammals: β -3 primer (GGACCTTCTCCTTCAAGGC), which is homologous to the terminal region of the Bovine endogenous retrovirus K1, BERVK 1). BERV β-3 and BERVK 1 belong to the group of Betaretrovirus and code the four viral proteins Gag, Pro, Pol, and Env [35-36].

PCR was performed used IRAP-PCR (Inter-Retrotransposon Amplified Polimorphism) method, allowing to amplify DNA regions flanked by the repeated primers.

Genomic DNA was prepared using commercial kit “DNA Extran-1” (Sintol, Russia). PCR was performed using the thermal cycler “Tertcik” (Russia), using the PCR-RV mixture (Sintol, Russia). The PCR cycling parameters were set as follows: 1) initialization at 94°C - 2 min; 2) denaturation at 94°C - 30 s; 3) annealing at 55°C - 30 s; 4) elongation at 72°C - 2 min; 5) final elongation at 72°C - 10 min; number of cycles - 35. 1.5% agarose gels stained by Ethidium Bromide were used to visualize the amplification results under the UV light. GeneRulerTM, 100bp DNA Ladder Plus (MBI Fermentas, USA) were used a molecular weight markers. Analysis was performed on the region of less than 1500 b.p.

Computational analysis was performed using computer program TFPGA [37]. The Polymorphic Information Content (PIC) was calculated for di-allelic loci using equation f=R1/2; where R - is the frequency of the animals within the group, amplification spectra of which has the DNA fragments of this length absent. R is considered as proportion of homozygotes relative to the recessive allele.

Results and Discussion

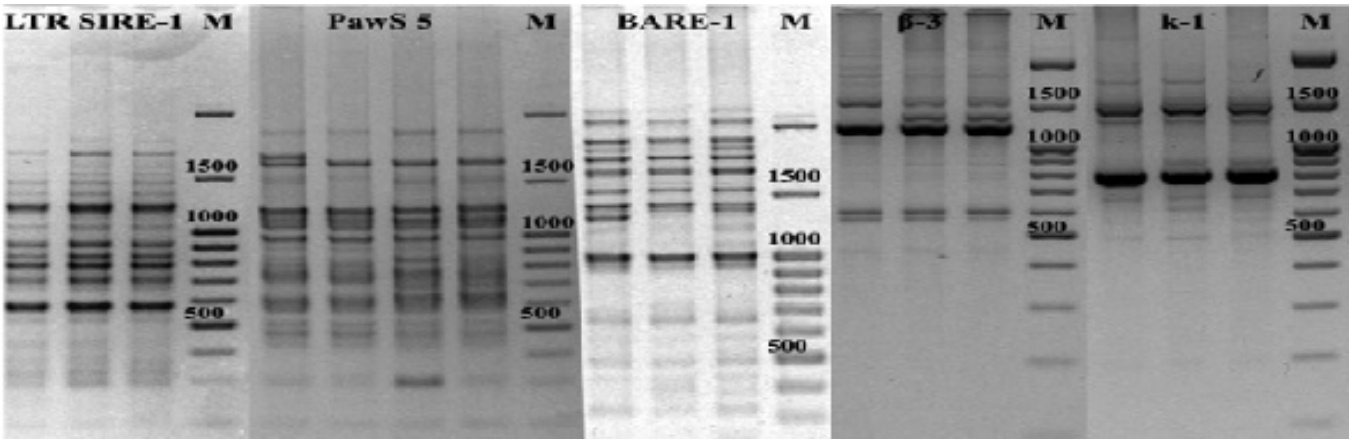
Genetic differentiation of local fat-tail sheep

For these studies we chose three different breeds (80 animals total): Karachaev, Kalmyk, Edilbaev (with two intra-breed types, Birlik and Suynduk). As a result of the IRAP-PCR study of the gene pools of these breads, each family was shown to have specific amplification spectra for each set of primers used. Differences between breeds for LTR SIRE-1 primer are less apparent that for the other primers (Figure 1 shows amplification spectra for representative animals from each breed).

The most heterogeneous breed turned out to be the Kalmyk sheep (in spectra of LTR SIRE-1 and PawS 5 - p=44%, 47%; average PIC=0.187, 0.174).

Genetic differentiation of local mountain horse breeds

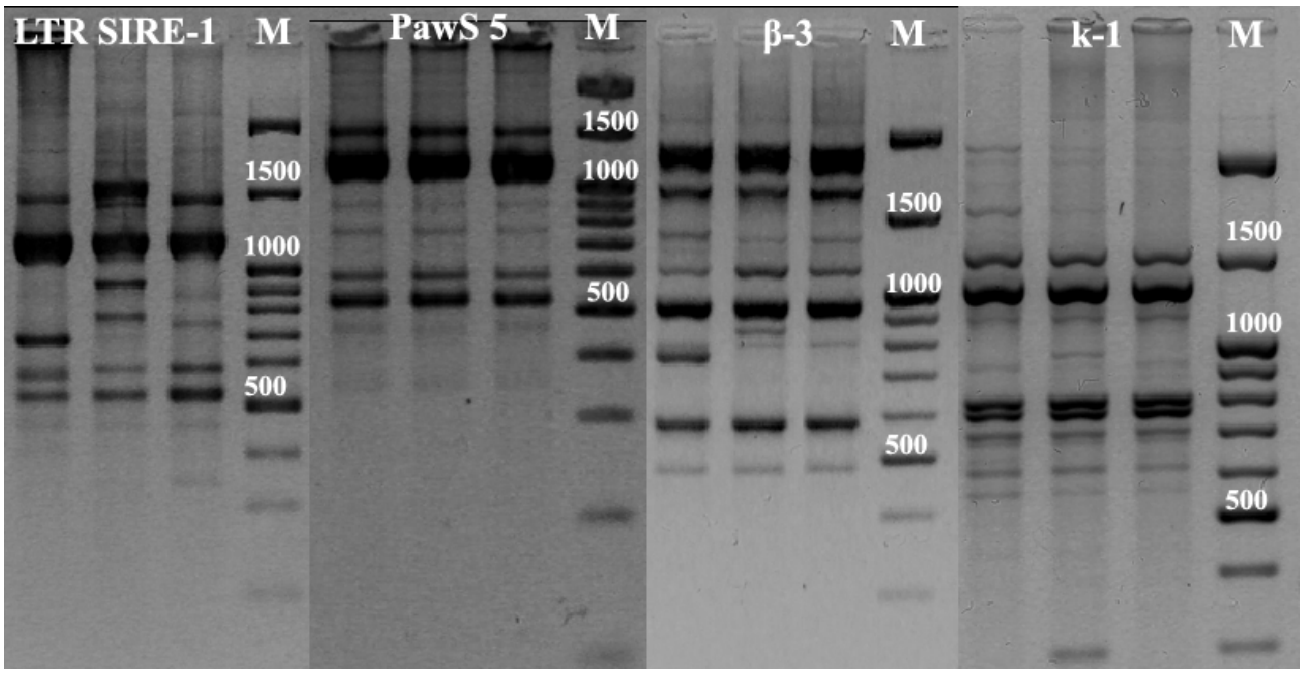
We have performed analysis of 88 blood samples from horses of various origins. The analysis includes blood samples from Karachaev breed, the Altai breed from three farms (“Djumbaev”,”Enchi”, “Chingiz”), as well as racing breeds (Orlov, Russian racing, American standard breed) [38]. The analysis showed that the amplification spectra using different set of primers did not significantly differ in the range of DNA fragment lengths between all the studied horse breeds (Figures 1-3).



Each panel depicts results of the indicated (at the top) set of primers.

In each of the SIRE-1, BARE-1, β-3, and k-1 panels, the three lanes from left-to-right represent Karachaev, Kalmyk, and Edilbaev breeds, respectively. In the PawS panel the first two lanes on the left represent Karachaev and Kalmyk breeds, respectively, and the two right-most lanes represent two different animals of Edilbaev breed. M - molecular weight marker

Figure 1: Amplification spectra of DNA fragments, obtained through genotyping of three sheep breeds.



Each panel depicts results of the indicated (at the top) set of primers.

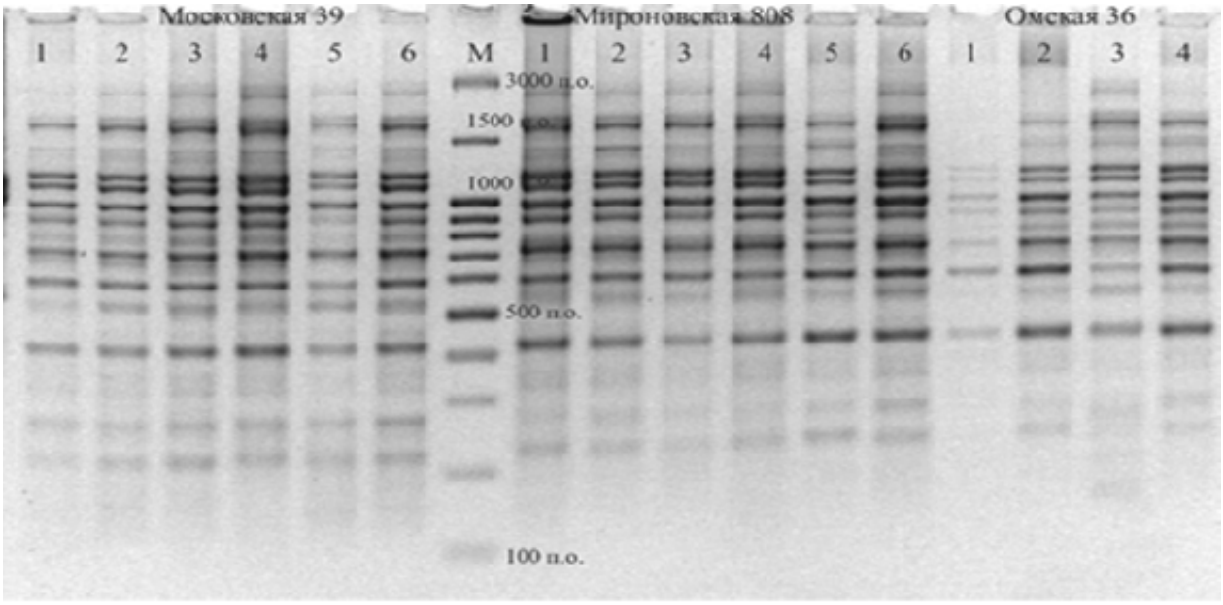
In each panel, the three lanes from left-to-right represent Karachaev, Altai, and Russian racing breeds, respectively. M - molecular weight marker

Figure 2: Amplification spectra of DNA fragments obtained through genotyping horse breed.

We note that the spectrum of PawS 5 primer is somewhat different, with distinct visualization of loci above 1500 b.p.

Each of the obtained amplification spectra is unique for each of the primers, and has a characteristic percentage of polymorphic loci and their distribution. The most polymprphic across all lengths were

amplification spectra of Altai horses from the farm "Djumbaev", obtained by using LTR SIRE-1 and PawS 5 primers. β-3 primers spectra yielded more than half of all loci in horses from "Enchi" and somewhat less polymorphic loci in the spectra of Altai horses from the third group are represented by frangments in the range from 500 b.p. to 1000 b.p, also, polymorphism of fragments above 1000 b.p. was seen only in the first group (18%). Karachaev horses differed in similarity of polymorphism across mid- and long-length fragments (from 5 to 10%). Spectra corresponding to k-1 primers were the same across all the studied breeds: mid-length range had 14% of polymorphic loci, long-range - 7%. Also, about a third of all loci within β-3 spectra were polymorphic. At the same time the intra-breed difference of Altai horses are not that evident in the β-3 spectra, with the exception of horses from "Chingiz" farm, which spectra are similar to Karachaev horses. The racing breeds were in the middle [38].



In first panel 1-6 lanes from left-to-right represent variety Moscow 39; the next panel 1-6 lanes - variety Mironov 808; the last panel 1- 4 lanes - variety Omsk 36, respectively. M - molecular weight marker

Figure 3: Amplification spectra of DNA fragments obtained through genotyping varieties of wheat with the use as primer in PCR the fragment of LTR SIRE-1.

Genetic differentiation of varieties of soft wheat and wild soybean

The analysis was performed using monocot *Triticum aestivum*, and dicot *Glycine soja* and *Glycin max* plants. Wheat was represented by two winter cereals - Moscow 39 - soft winter, Mironov 808 - soft winter wheat, derived from spring cereal, and also one soft cereal - Omsk 36. Soybean was represented by five populations of wild Ussurian soy (*G. soja*, Primorsky krai) and the weed variety (*G. max*, China). We found that more than third of all fragments (38%) in the amplification spectra of wheat using LTR SIRE-1 can be used to differentiate varieties (Figure 3), and about a half (47%) of loci in the respective amplification spectra of wild soy (*G. soja*). One third of all fragments are species-specific, which distinguishes *G. soja* from *G. max* [38].

Previously we suggested that one of the sources of genetic variability of domesticated species is genetic destabilization due to retrotransposition as result of inbreeding [19]. In support of this hypothesis, we note that highly inbred line of laboratory mice there are significant differences in the spectra of mobile elements [39]. In order to estimate possible influence of inbreeding on the polymorphism of DNA fragments flanked by inverted repeats of endogenous retroviruses, we compared the respective amplified spectra of muskox (Ovibos moschatus), which were introduced into the northern Russia, which numbers and inbreeding is controlled.

We have investigated genomic DNA of 100 muskox animals from three introduced populations - initial, native to Greenland, Taymyr population, and the most inbred - from the Wrangel Island [40]. In addition, we compared the three current population with the ancient muskox population (5 samples) that live on Taymyr about 10,000 years ago in Yakutia 40,000 years ago.

For ISSR-PCR we used (AG) 9C, (GA) 9C and (GAG) 6C, for IRAP-PCR we used LTR SIRE-1 и PawS 5. Average PIC index was calculated to reflect the proportion of heterozygotes. The obtained data is shown in Table 1.

Primer	Ancient animals from Taymyr and Yakutia		Ancient animals from Yakutia		Extant animals from Wrangel Isl, Taymyr pens, and Greenland		Extant Taymry		Extant muskox from Greenland		Extant muskox from Wrangel	
	Polymorphic loci %	PIC	Polymorphic loci, %	PIC	Polymorphic loci, %	PIC	Polymorphic loci, %	PIC	polymorphic, %	PIC	Polymorphic loci, %	PIC
(AG)9C	89.3	0.312	78.i	0.311	25.0	0.058	8.3	0.037	16.7	0.067	0.0	0.000
(GA)9C	77.8	0.278	63.0	0.233	53.9	0.200	46.2	0.143	38.5	0.174	53.9	0.186
(GAG)6C	93.5	0.317	77.4	0.299	33.3	0.094	11.1	0.039	22.2	0.090	22.2	0.087
Sum ISSR	87.2	0.303	73.3	0.282	38.2	0.122	23.5	0.078	26.5	0.114	26.5	0.094
LTR SIRE-1	83.3	0.298	66.7	0.242	75.0	0.266	41.7	0.176	8.3	0.039	75.0	0.296
PawS 5	54.5	0.118	54.5	0.143	14.3	0.055	14.3	0.055	0.0	0.000	14.3	0.062
Sum IRAP	75.6	0.250	63.4	0.215	52.6	0.188	31.6	0.131	5.3	0.025	52.6	0.210

Table 1: Polymorphic loci percentages and PIC coefficients for different population of extant and ancient muskoxes. For each of the groups of the animals examined Polymorphic loci % and polymorphic information content (PIC) values are shown. Raws in the table correspond to different primers used.

From Table 1 it is evident that, overall, the extant muskox are significantly less heterogeneous compared to the ancient populations. In the extant animals using the ISSR-PCR markers, the polymorphic loci percentage reaches 38.2% and PIC of 0.112; with the IRAP-PCR markers these values were at 52.6% and 0.188, respectively. The ancient animals, in contrast, with the ISSR-PCR markers had polymorphic percentage 87.2% and PIC of 0.303; with the IRAP-PCR markers these values were at 75.6% and 0.250, respectively. Notably, these differences between extant and ancient muskoxes are more apparent with the ISSR-PCR markers rather than IRAP-PCR, which might be related to higher initial heterogeneity of the ancient population.

Intriguingly, in the extant muskoxes in parallel to the increase in the inbreeding from the native Greenland population to the most inbred Wrangel population, as expected, we see decrease of PIC according to ISSR-PCR markers; while PIC according to IRAP-PCR markers increases. For instance, ISSR-markers in Greenland population give PIC=0.11; in Taymyr population=0.08; in Wrangel=0.09. In contrast, the IRAP markers in Greenland population give PIC=0.02; in Taymyr population=0.13; in Wrangel=0.21.

The studied groups of muskoxes, in general, show discordant tendencies of the decrease in heterozygocity with the increase in inbreeding using different marker types: there is a tendency of increase in heterozygocity showed by IRAP-PCR markers and at the same time its decrease showed by ISSR-PCR markers. In other words, with inbreeding polymorphism of mobile elements increases, while polymorphisms of other genetic elements decreases. These data are consistent with our hypothesis that as a result of inbreeding, which is typical for domesticated species during artificial selection, may lead to the activation of transpositions in their genomes, which, in turn, may lead to increase in genetic variability. In essence, this variability is the "domestication cost" - accumulation of genetic load, as discussed in several publications ([10], for example).

In summary, our data along with data accumulated by other groups up to date indicates that one of the main sources of the unexpectedly high intra-species genetic variability of domesticated animals and plants could be the increased tolerance to the incorporation of DNA of exogenous retroviruses and also activation of mobile genetic elements as a result of inbreeding (self-pollination in the case of agricultural plants). We await further experiments and thorough validation of this idea in the future.

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References

1. Piras D, Doro MG, Casu G, Melis PM, Vaccargiu S, et al. (2012) Haplotype affinities resolve a major component of goat (Capra hircus) MtDNA D-loop diversity and reveal specific features of the Sardinian stock. PLoS One 7: e30785.
2. Bauchet G, Munos S, Sauvage C, Bonnet J, Grivet L, Causse M (2014) Genes involved in floral meristem in tomato exhibit drastically reduced genetic diversity and signature of selection. BMC Plant Biol 14: 279.
3. Rong J, Lammers Y, Strasburg JL, Schidlo NS, Ariyurek Y, et al. (2014) New insights into domestication of carrot from root transcriptome analyses. BMC Genomics 15: 895
4. Mandel JR, McAssey EV, Nambeesan S, Garcia-Navarro E, Burke JM (2014) Molecular evolution of candidate genes for crop-related traits in sunflower (Helianthus annuus L). PLoS One 9: e99620.
5. Andersson L, Archibald AL, Bottema CD, Brauning R, Burgess SC, et al. (2015) Coordinated international action to accelerate genome-to-phenome with FAANG, the Functional Annotation of Animal Genomes project//Genome Biology 16: 57.
6. De Simoni Gouveia JJ, Da Silva MVG, Paiva SR, De Oliveira SMP (2014) Identification of selection signatures in livestock species. Genetics and Molecular Biology 37: 330-342.

7. Moon S, Kim TH, Lee KT, Kwak W, Lee T, et al. (2015) A genome-wide scan for signatures of directional selection in domesticated pigs. BMC Genomics 16: 130.
8. Evin A, Dobney K, Schafberg R, Owen J, Vidarsdottir US, et al. (2015) Phenotype and animal domestication: A study of dental variation between domestic, wild, captive, hybrid and insular Sus scrofa. BMC Evolutionary Biology 15: 6.
9. Metzger J, Tonda R, Beltran S, Águeda L, Gut M, et al. (2014) Next generation sequencing gives an insight into the characteristics of highly selected breeds versus nonbreed horses in the course of domestication. BMC Genomics 15: 562.
10. Schubert M, Jónsson H, Chang D, Der Sarkissian C, Ermini L, et al. (2014) Prehistoric genomes reveal the genetic foundation and cost of horse domestication. Proc Natl Acad Sci U S A 111: E5661-9.
11. Porto-Neto LR, Reverter A, Prayaga KC, Chan EKF, Johnston DJ, et al. (2014) The Genetic Architecture of Climatic Adaptation of Tropical Cattle. PLoS ONE 9: e113284.
12. Porto-Neto LR, Sonstegard TS, Liu GE, Bickhart DM, Da Silva MV, et al. (2013) Genomic divergence of zebu and taurine cattle identified through high-density SNP genotyping. BMC Genomics 14: 876.
13. Ramey HR, Decker JE, McKay SD, Rolf MM, Schnabel RD, et al. (2013) Detection of selective sweeps in cattle using genome-wide SNP data. BMC Genomics 14: 382.
14. Ghosh S, Qu Z, Das PJ, Fang E, Juras R, et al. (2014) Copy Number Variation in the Horse Genome. PLoS Genet 10: e1004712.
15. Liu GE, Hou Y, Zhu B, Cardone MF, Jiang L, et al. (2010) Analysis of copy number variations among diverse cattle breeds. Genome Research 20: 693-703.
16. Revay T, Quach AT, Maigne L, Sullivan B, King WA (2015) Copy number variations in high and low fertility breeding boars. BMC Genomics 16: 280.
17. Wilkins AS, Wrangham RW, Fitch WT (2014) The "Domestication Syndrome" in Mammals: A Unified Explanation Based on Neural Crest Cell Behavior and Genetics. Genetics 197: 795-808.
18. Albert FW, Somel M, Carneiro M, Aximu-Petri A, Halbwax M, et al. (2012) A Comparison of Brain Gene Expression Levels in Domesticated and Wild Animals. PLoS Genet 8: e1002962.
19. Glazko V, Zybaylov B, Glazko T (2014) Domestication and Genome Evolution. International Journal of Genetics and Genomics2: 47-56.
20. Wiener P, Wilkinson S (2011) Deciphering the genetic basis of animal domestication. Proc R Soc B 278: 3161-3170.
21. Rischkowsky D (2007) The state of the world's animal genetic resources for food and agriculture. B Pilling (editors) FAO, Rome.
22. Diamond J (2002) Evolution consequences and future of plant and animal domestication. Nature 418: 700-707.
23. Garcia-Etxebarria K, Sistiaga-Poveda M, Jugo BM (2014) Endogenous retroviruses in domestic animals. Curr Genomics 15: 256-65.
24. Oliveira SG, Bao W, Martins C, Jurka J (2012) Horizontal transfers of Mariner transposons between mammals and insects. Mob DNA 3: 14.
25. Walsha AM, Kortschaka RD, Gardnerb MG, Terry Bertozzia T, Adelson DL (2013) Widespread horizontal transfer of retrotransposons//PNAS USA 110: 1012-1016.
26. Chalopin D, Naville M, Plard F, Galiana D, Volff JN (2015) Comparative Analysis of Transposable Elements Highlights Mobilome Diversity and Evolution in Vertebrates. Genome Biol Evol 7: 567-580.
27. Bao W, Jurka J (2013) Homologues of bacterial TnpB_IS605 are widespread in diverse eukaryotic transposable elements//Mobile DNA 4: 12.
28. Benachenhou F, Sperber GO, Bongcam-Rudloff E, Andersson G, Boeke JD, Blomberg J (2013) Conserved structure and inferred evolutionary history of long terminal repeats (LTRs). Mobile DNA 4: 5.
29. Llorens C, Munoz-Pomer A, Bernad L, Botella H, Moya A (2009) Network dynamics of eukaryotic LTR retroelements beyond phylogenetic trees. Biology Direct 4: 41.
30. Ahmed M, Liang P (2012) Transposable elements are a significant contributor to tandem repeats in the human genome. Comp Funct Genomics 2012: 947089
31. Behura SK, Severson DW (2013) Association of microsatellite pairs with segmental duplications in insect genomes. BMC Genomics 14: 907.
32. Sharma A, Wolfgruber TK, Presting GG (2013) Tandem repeats derived from centromeric retrotransposons. BMC Genomics 14: 142.
33. Bousios A, Darzentas N (2013) Sirevirus LTR retrotransposons: phylogenetic misconceptions in the plant world. Mobile DNA 4: 9.
34. Rogowsky PM, Liu JY, Manning S, Taylor C, Langridge P (1992) Structural heterogeneity in the R173 family of rye-specific repetitive DNA sequences. Plant Mol Biol 20: 95-102.
35. Baba K, Nakaya Y, Shojima T, Muroi Y, Kizaki K, et al. (2011) Identification of Novel Endogenous Betaretroviruses Which Are Transcribed in the Bovine Placenta. J Virol 85: 1237-1245.
36. Xiao R, Kim J, Choi H, Park K, Lee H, Park C (2008) Characterization of the Bovine Endogenous Retrovirus β3 Genome. Mol Cells 25: 142-147
37. Miller MP (1997) Tools for population genetic analyses (TFPGA) 1.3: A Windows program for the analysis of allozyme and molecular population genetic data. Computer software distributed by author.
38. Elkina MA, Glazko VI (2012) The fragments of homologies of endogenous retroviruses in the genomes of plants and animals. Agricultural biology 5: 35-43.
39. Nellaker C, Keane TM, Yalcin B, Wong K, Agam A, et al. (2012) The genomic landscape shaped by selection on transposable elements across 18 mouse strains. Genome Biology 13: R45.
40. Glazko VI, Bardukov NV, Pheophilov AV, Sipko TP, Elkina MA, et al. (2012) Polymorphism of ISSR and IRAP markers in genomes of musk-oxen (Ovibos moschatus)and horse (Equus caballus) of Altai breed. Izvestia of Timiryazev Agricultural Academy Special Issue: 16-26.