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# IDENTIFICATION OF "SELECTION SIGNATURES" IN PIGS AND WILD BOARS
(review)

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## Abstract

The pig is one of the few species that has living wild ancestors, which provides a unique opportunity to track the evolutionary history of mammals and determine the "selection signatures" caused by both domestication and natural selection (K. Chen et al., 2007). Animal selection leads to changes in certain regions in the genome associated with economically significant traits, adaptation to climate and stress conditions, immune response and resistance to diseases, and as a result of its pressure, traces are formed in the genome of animals (S.R. Keller et al., 2008), known as selection signatures (M. Kreitman, 2000). Identification of selection prints attracts special attention of evolutionary geneticists, since it can serve as a source of information, ranging from basic knowledge about evolutionary processes to functional information about genes/genomic regions (C. Schlцtterer, 2003; C. Horscroft et al.). The purpose of this review is to summarize approaches used to identify "selection signatures", as well as to analyze the detected traces of selection in domestic pigs and wild boar. The development of modern methods of full-scale research has significantly expanded the arsenal of tools that allow searching for regions subjected to selection pressure at a fundamentally new level. Analysis of data obtained using full-genome resequencing (C.J. Rubin et al., 2012; X. Li et al., 2017), full-genome genotyping on biochips of different densities (M. Huang et al., 2020; M. Mucoz et al., 2019), RADseq (Y. Li et al., 2017), RNA-seq (M. Li et al., 2017; Y. Yang et al., 2018), GBS (Y. Ma et al., 2018; K. Wang et al., 2018) is used to search for selection prints in *Sus scrofa*. Methods are based on scanning areas of homozygosity, as well as evaluating differences in the frequency of alleles or haplotypes between populations or generations within a population. The most commonly used statistical methods for identifying selection prints are extended haplotypic homozygosity (EHH) (P.C. Sabeti et al., 2002), integrated haplotype estimation (iHS) (B.F. Voight et al., 2006), runs of homozygous segments (ROH) (J. Gibson et al., 2006), Fst-statistics (R.C. Lewontin, J. Krakauer, 1973), haplotype-based analysis (hapFLK) (M.I. Fariello et al., 2013), composite selection signal method (CSS) (I.A. Randhawa et al., 2014), and a combination of these methods. Breeding models in pig breeds differ depending on their evolution and breeding history, so studying the "selection signatures" of a large number of different breeds will help to better understand the genetic variations underlying the traits of interest. Based on these methods, large-scale fingerprint scans of diversifying selection have been successfully applied to domestic pigs. In most cases, the research was aimed at studying the evolutionary and selection mechanisms of the genome of Chinese pigs (X. Li et al., 2017; M. Chen et al., 2018). The research found genomic regions that contribute to adaptation to various climatic conditions (R.J. Cesconeto et al., 2017), as well as candidate genes associated with growth, development (K. Wang et al., 2018), reproductive traits (Z. Zhang et al., 2018) and certain aspects of the immune response (S. Yang et al., 2014). Full-genomic research of domestic resources (A. Traspov et al., 2016) showed that pig populations bred on the territory of the Russian Federation, including local ones, are a cultural achievement of domestic animal science and have their own unique structure, even though they

originated with the participation of imported breeds. This may be due to several factors, including differences in origin, long periods of genetic isolation, and differences in climate and food resources. However, domestic breeding resources remain poorly studied at the moment. Thus, the proposed approaches designed to identify "selection signatures" in pigs bred on the territory of the Russian Federation and wild boar can be used to search and analyze the detected traces of selection in domestic pigs and wild boar of domestic origin.

Keywords: pigs, selection prints, domestication, genome-wide genotyping, haplotype, homozygosity

The pig, which belongs to the mammalian order *Artiodactyla*, is one of the first domesticated animals that is important in agriculture as a source of nutritious protein. The pig is also of interest as a biomedical model with high anatomical and immunological similarity to humans [1]. It is one of the few species that have living wild ancestors, which provides a unique opportunity to track the evolutionary history of mammals and determine the "selection signatures" caused by both domestication and natural selection [2].

Natural selection is the process by which populations can adapt, survive, and reproduce in their environment. Individuals with traits that improve viability and reproductive qualities can pass these on to their descendants, which over time affects the increase in representation of useful traits in the population [3]. Individuals with a favorable allele have increased adaptability to environmental conditions and better chance for reproduction compared to individuals lacking this allele [4].

The occurrence of selection creates deviations from the expectations of the neutral theory in models of molecular variability [5]. Each form of both natural and artificial selection causes specific changes in the dependent loci and associated neutral loci. Animal selection leads to changes in certain areas of the genome that affect economically significant traits as well as characteristics related to climate and stress adaptation, immune response, and disease resistance. Therefore, as a result of selection pressure, there are traces formed in the genome of animals [6], which are known as "selection prints" ("signature of selection") that can be used to identify loci subjected to selection pressure [7]. The search for selection signatures has attracted special attention from evolutionary geneticists, who can obtain both basic knowledge about evolutionary processes and functional information about genes/genomic regions [8, 9]. In addition, it provides an opportunity to better understand the history of populations and genetic mechanisms that affect the phenotypic differentiation of wild and domestic animals [10]. Determining the genes that are under selection pressure will make it possible to detect causal mutations in regions previously identified through quantitative trait loci (QTL) mapping experiments, and genes associated with environmental traits (such as adaptation) that are difficult to find experimentally [5]. Such studies will be useful when searching for genes or gene networks that play an important role in the formation of the same phenotypic traits but vary among breeds. They can also reveal the genes involved in the domestication process [8, 11].

Domestic pigs (*Sus scrofa*) have significant differences in morphological, behavioral, and environmental characteristics [12]. The use of this species in a wide variety of production systems around the world has led to a huge variety of breeds, each of which is adapted to specific conditions [5]. The search for signature of selection in pigs will help to show the genetic determination of quantitative traits and the mechanisms of adaptive reactivity of the species.

The purpose of this review is to describe the approaches used to identify signature of selection, as well as to analyze the detected selection traces in domestic pigs as compared to wild boar.

With the development of modern genome-wide research methods, the variety of tools that allow searching for regions that are subjected to selection pressure has significantly expanded. Full-genome resequencing to identify "selection prints" in *S. scrofa* [13, 14] was performed using biochips of different densities: Affymetrix Axiom Pig1.4M (Affymetrix™, Thermo Fisher Scientific Inc., USA) [15], GeneSeek® Geno-mic Profiler (GGP) 70 K HD Porcine chip (Illumina, Inc., USA) [16-18], Illumina Porcine SNP60 BeadChip (Illumina, Inc., USA) [19-21], and also restriction-site associated DNA sequencing (RADSeq) [22], RNA sequencing (RNA-seq) [23, 24], and genotyping by sequencing (GBS) [25, 26].

Recognizing the molecular traces left by different types of selection is the main task in identifying the parts of the genome that are being selected. In this case, the neutral theory serves as the basis for statistical tests designed to detect selection traces. However, in natural populations, some assumptions of the neutral theory can be violated (for example, as a result of population growth, migration, and "bottleneck"), which leads to signals that mimic selection traces [5]. The interaction between different types of selection and between selection and demographic factors can shift the traces of such processes left in the genome [5, 7, 27]. In this regard, it is worth noting that when detecting traces of breeding in farm animals, a significant number of false positive results are expected due to genetic drift and the founder effect, which are especially important in the formation and development of breeds [28]. It is also important to distinguish positive selection prints from those formed as a result of neutral evolution, and to select appropriate statistical tests and software for screening them to determine the genomic regions involved in adaptation processes [29].

There are several approaches for detecting selection signatures. As a rule, they are based on the search for homozygous regions and the assessment of differences in the frequency of alleles or haplotypes between populations or generations within the population [30]. Several methods were developed for the statistical processing of the data obtained.

Extended haplotype homozygosity (EHH) [31-33] is the maximum value for a small number of different haplotypes with unequal frequency distribution. This test reveals selection traces by comparing the base (main) haplotype, which is characterized by high frequency and extended homozygosity, with other haplotypes at the selected locus.

The integrated haplotype score (iHS) [34] was proposed for genomic scale work based on information obtained using high-density single nucleotide polymorphism (SNP) chips. The iHS value shows how unusual the haplotypes around the SNP are compared to the genome.

Runs of homozygosity (ROH) [10] were first introduced by Gibson et al. [35] as adjacent homozygous segments in the genome that are present in an individual due to transmission of identical haplotypes from parents to offspring. The frequency of ROH varies widely within and between chromosomes; along with hot spots ("islands"), ROH is met with cold spots ("deserts") [36]. The reasons for this are of great interest, since the distribution of ROH across chromosomes is not random [37, 38]. The number of ROHs and their size distribution are important determinants of long-standing and recent events in the population. Long sections of ROH appear more often in regions with low recombination located in the middle of the chromosome, and the smallest ROH with higher density is distributed in the direction of telomeric regions [37]. Accordingly, the presence of long sections of ROH indicates a recent common ancestor. Conversely, shorter ROH regions indicate greater temporal distance from the common ancestor. ROH identification and characterization provide insight into how population structure and

demographic events evolved over time. In addition, ROH has recently been increasingly used in the search for genome regions associated with selection pressure. It is assumed that most of the genome is in the selection process, while all functional sites in the genome are under the pressure of selection [39] or adaptive evolution [40]. One strength of ROH analysis is that long homozygous segments can be reliably identified even with relatively low marker densities [10].

Haplotype-based analysis (hapFLK) [41-43], unlike most existing statistical data processing methods, accounts for the hierarchical structure of the selected populations. Using computer modeling, Fariello et al. [44] showed that using information about haplotypes and the hierarchical structure of populations significantly increases the power of detecting selected loci, and combining them in hapFLK statistics provides even greater efficiency. It has also been demonstrated that the hapFLK method produces reliable results in bottleneck and migration conditions, and in many other cases exceeds the existing approaches.

The composite selection signals (CSS) method [45-47] combines three different approaches: determining the fixation index ($F_{ST}$) of population differentiation (allows the detection of selection traces from genetic polymorphism data by paired comparison of two modern populations); evaluating changes in the frequency distribution of derived allele frequencies (ΔDAF) or changes in the direction of the selected allele frequency (ΔSAF); and statistics of extended haplotype homozygosity (EHH), depending on the frequency of the allele and the strength of the linkage disequilibrium (LD) with neighboring loci.

The FST, first defined by Wright [48, 49], is a measure that uses differences in allele frequencies to determine genetic differentiation between populations or generations [50]. Akey et al. [51] proposed using loci in the tails of the empirical FST distribution as potential selection targets.

Tests based on LD [25] are used to detect selection traces in pigs. Usually, several breeds are compared, and the genetic basis of various characteristics of the breed, such as productivity [52-54], morphology [55], and adaptation to local conditions such as climate [56, 57], are put at the forefront. Selection signatures associated with growth traits, reproductive qualities, coat color, or ear shape were found, and several genes that significantly influence these traits were identified [18, 13]. However, the selection models of pig breeds differ depending on their evolution and demographic history, therefore, studying the selection signatures of a large number of breeds will help to better understand the genetic mechanisms that cause the manifestation of interesting traits.

Attempts were made to analyze the mechanisms underlying the phenotypic differentiation of pigs caused by selection pressure [58-60]. Gurgul et al. [61] found selection traces at the whole genome level in three native populations of pigs (Puławska, Złotnicka White and Złotnicka Spotted) and the Polish Landrace. To identify the selection prints in the analyzed breeds, they applied the method based on FST and aimed at detecting selection diversification among breeds, as well as relative extended haplotype homozygosity (REHH) statistics [31, 62], allowing the detection of permanent selection in the breed. It was shown that both FST and REHH statistics are useful for detecting selection prints [63] and largely complement each other. The REHH test can detect selection prints within breeds with high efficiency and is more accurate in the case of ongoing selection, whereas the $F_{ST}$ is useful for detecting selection prints among breeds represented mainly by loci that are differentially fixed in different breeds [64].

Li et al. [65] found selection prints in native Chinese pigs by comparing variations using the non-equilibrium coupling method (LD) [66]. Yang et al. [19] performed genome-wide scanning of selection prints in Chinese local and commercial breeds using High-FST and identified 81 candidate genes with a high

degree of confidence of positive selection. In addition, the gene network analysis results showed that genes of traits subjected to positive selection were mainly involved in the development of tissues and organs, and in the immune response [17]. Rubin et al. [13] used pig genome sequencing (S.scrofa10.2) [67] and re-sequencing of the entire genome of domestic pigs and boars to identify loci that were subjected to selection pressure during and after domestication. This study was based on the search for genetic variants with noticeable differences in the frequency of alleles between populations of pigs and wild boar. The strongest selection fingerprint (ZHp = -5.82) was present on the 1st chromosome of *S. scrofa* (SSC1) for the locus that includes the *NR6A1* (nuclear receptor 6 A1) gene. Also significant was the region on SSC4 (ZHp = -5.77), which includes *PLAG1* (pleomorphic adenoma gene 1), and the region on SSC8 (ZHp = -5.29), which covers the entire coding region of the ligand-dependent corepressor-like nuclear receptor (*LCORL*). The *NR6A1* gene is associated with the number of vertebrae in pigs (boar usually has 19, and pigs have up to 21) [68]. The melanocortin receptor 1 (*MC1R*) gene was identified as an artificial selection gene associated with coat color in domestic pigs in China [69].

Genetic adaptation to different climatic conditions has formed distinct thermoregulatory mechanisms for high and low temperatures, which are mainly manifested in pigs of local breeds. To identify genomic loci that contribute to adaptation to various climatic conditions, Ai et al. [57] studied Chinese pigs from the southern and northern regions. A total of 774 regions located on autosomes and the X chromosome were identified. Ontology analysis identified genes that are involved in biological processes that contribute to maintaining thermoregulation during heat or cold. These processes are associated with hair development, differentiation of neurons in the thalamus, kidney development, energy exchange, and blood circulation. For example, genes involved in hair cell differentiation (*ATOH1*, *JAG1*, and *RAC1*) and maturation of hair follicles (*BARX2* and *TBC1D8*) were isolated. This is consistent with the fact that southern Chinese pigs have sparse, short hair, which facilitates heat loss, whereas northern Chinese pigs usually have long, thick hair that forms a dense coat. The genes involved in the differentiation of neurons in the thalamus (*DLX1*, *DLX2*, *RAC1*, *ROBO1* and *SALL1*) are described, and explain the important role of the nervous system in acclimatization. The *BMP4*, *BMP7*, *MYC*, *SALL1*, *SPRY1*, and *KLHL3* genes are responsible for processes that affect kidney development, which may be associated with a tendency to increase kidney mass at low ambient temperatures and decrease it at high [70]. Genes related to blood circulation are also known, and are involved in the development of arteries (*BMP4*, *CITED2*, and *JAG1*), and the embryonic heart tube (*CITED2*, *INVS*, *RYR2*, *SUFU*, and *TBC1D8*). In the process of temperature adaptation, biological mechanisms that ensure blood flow play an important role, since heat stress can lead to an increase in the number of platelets and blood viscosity, which in turn increases the risk of cerebral and coronary thrombosis [71]. In southern Chinese pigs, a missense-mutation in the *VPS13A* gene was found to reduce the risk of thrombosis by modulating the number of platelets and blood viscosity.

The search for selection signatures related to climate conditions was performed in Brazilian pigs by Cesconeto et al. [72]. As a result of their work, genomic regions were identified that contribute to the adaptation of pigs to various environmental conditions: temperature, precipitation, and solar radiation.

Traditional breeding programs for the most common commercial pig breeds (Large White, Yorkshire, Landrace, Duroc, and Pietren) focus mainly on growth rates and feed conversion. Thus, Wang et al. [25] found in the Landrace

and Yorkshire breeds, 540 potential regions (50 kb) controlling these traits, which contained 111 genes.

Most candidate genes were associated with growth, development, and other aspects of the immune response (*COL11A1*, *GHR*, *IGF1R*, *IGF2R*, *IFNG*, and *MTOR*), and only a few were associated with meat quality (*ACACA* and *MECR*). Chinese pigs are characterized by slow growth rates, the ability to quickly accumulate fat deposits, high meat quality indicators, and earlier puberty. A study of selection prints performed on Large White pigs [65], Chinese breeds, and South American native pigs [73, 74] identified four genomic regions on the 7th, 9th, 13th, and 14th chromosomes. For Chinese pigs, a significant region localized on SSC14 included the genes *MORC2*, *SMTN*, *INPP5J*, *PLA2G3*, and *RNF185* associated with the content of linoleic acid [75, 76], one of the polyunsaturated fatty acids, the content of which is characterized by a high positive correlation with the flavor of pork meat [77, 78]. This region was also associated with the early sexual maturity characteristic of Chinese pigs [79]. In the study of Li et al. [65] selection signatures were also identified for Large White pigs, located on the 7th and 9th chromosomes. One interesting gene found in these regions is *ADAMTSL3* (SSC7], which is a candidate gene that determines the length of the trunk [80]. In the works previously conducted by Wilkinson et al. [20] and Li et al. [81], this gene was also recognized as a significant selection signature for European commercial breeds of pigs.

Zhang et al. [11] studied the genetic basis of phenotypic differences between Chinese and Western pig breeds. Numerous genes (*IGF1R*, *IL1R1*, *IL1RL1*, *DUSP10*, *RAC3*, *SWAP70*, *SNORA50*, *OR1F1*) related to growth, immunity, smell, reproduction, and meat quality were identified as differentiated candidate genes that could be associated with phenotypic differences in Western and Chinese pigs. Evaluation of FST signals allowed us to identify differentiated features in Chinese pig breeds. There were 75 genes near strong FST signals. The most significant SNPs were located near the *JPH3* (SSC6) gene associated with skatole content [82] and meat quality indicators [83]. On the 4th chromosome, the signal was detected in the *ZFPM2* gene, for which Zhao et al. [84] established a connection with pig scrotal hernias. On the 15th chromosome, a signal was detected near the *CNTNAP5* gene, previously noted by Rohrer et al. [85] as a candidate gene for the number of vertebrae in pigs. Expression mapping helped to identify the genetic basis of phenotypic features of Western pigs (growth, feed intake, meat yield, fat thickness) and Chinese pigs (good adaptation, immunity, high quality of meat, and reproductive qualities).

Wang et al. [25] showed that pigs of the Taihu, Meishan, Fengjing, Shawutou, Erhualian, Jiaxing Black, and Mizhu breeds were subjected to less intensive selection in contrast to Western commercial breeds. Different regions of their genomes were subjected to selective pressure. For Western pigs, more pressure was directed to the areas that cause signs of fattening and meat production (growth indicators, fat thickness, precocity, and muscle depth). The selection signatures showed a significant number of genes involved in lipid metabolism and reproduction, which is expected, given the breeding programs of commercial breeds of pigs aimed at increasing fattening productivity and reproductive function. In the Taihu pig genomes, most regions were associated with reproduction and relatively high disease resistance.

The unique feature of the Laiwu pig breed, associated with a high content of intramuscular fat, led to their use as model animals in determining the selection prints for fat deposition in muscles and identifying genes associated with the formation of intramuscular fat. In the work of Chen et al. [86], the search for genomic regions in pigs of Laiwu ($n$ = 50) and Yorkshire ($n$ = 52) breeds was

performed using three methods. The length of the genomic regions identified by at least one method was 465 Mb. On SSC8, one region (2.75-3.00 Mb) was identified in all three ways. From the results of at least two methods, 175 candidate regions were identified and unevenly distributed; most are located on SSC8 (86 regions) and none on SSC12. A total of 438 genes were identified in these regions, including *NPY1R*, *NPY5R*, *PIK3R1*, and *JAKMIP1* associated with feed intake and fat deposition, *ESR1* and *PTHLH* associated with reproductive functions, and *CXCL2*, *CXCL8*, and *TLR2* associated with immune responses. In addition, approximately 25% of the signals were registered in intergenic regions, which indicates an important function of non-coding sequences in the selection process. An additional study of the functions of annotated genes showed that the most significant genes involved in the regulation of metabolic processes, cell proliferation, feeding behavior, immunity, pathways for transmitting signals of the epidermal growth factor receptor, and neuropeptide. It should be noted that in other studies, some of these functional genes have also been observed as being under selection pressure or related to energy balance.

Zhu et al. [87] identified 14 genomic regions associated with selection during domestication in Chinese pigs (16 boars were selected from 7 locations in China and 54 individuals from 9 Chinese native breeds: Bamaxiang, Erhualian, Hetao, Jinhua, Luchuan, Wuzhishan, Neijiang, Bamei, Baoshan). Products of genes localized in these regions are functionally involved in the metabolic processes that ensure growth and development, reproduction, smell, behavior, and activity of the nervous system of animals. The most interesting genes are *TBX19* (involved in metabolic changes and development of Chinese domestic pigs) and *AHR* (associated with sow reproduction).

Based on the analysis of functional enrichment of the regions of the "selection signatures" [88], 449 protein-coding genes were identified in Rongchang pigs. Among them, 10 genes (*CNTN4*, *DLL3*, *GHSR*, *LHX5*, *MAP1B*, *MBP*, *METRN*, *NUMBL*, *TNFRSF12A*, and *REST*) were identified in supporting brain development, neuron function, and behavior. These results support the view that mutations associated with reduced fear and aggression towards humans are at the heart of domestication [89]. In addition, four genes (*CYP2A6*, *GMPS*, *UPB1*, and *UPP2*) were identified that are responsible for the metabolism of narcotic drugs, which is probably due to the constant exposure of domestic pigs to high doses of chemicals.

Studies of local pig breeds carried out in several countries have shown [90] that many of them retain unique features and differ from the main commercial breeds, such as the Large White and Landrace breeds. This may be due to differences in the origin of populations, long periods of genetic isolation, and differences in climate and available food between Western Russia, Belarus, Ukraine, and Western Europe [90].

Therefore, the analysis of the literature data demonstrated a clear interest in the in-depth study of the genetics of the *Sus scrofa* species. Various genomic and statistical methods based on the search for homozygosity regions and the estimation of differences in the frequency of alleles or haplotypes between populations have been tested. Most often, extended haplotypic homozygosity, integrated assessment of haplotypes, identification of extended homozygous segments, FST-statistics, haplotype-based analysis, the method of composite selection signals and their combination are used for the analysis of selection prints in pigs and boars. Studying the selection prints of many different breeds will help to better understand the genetic variations underlying the traits of interest. However, most of the work is carried out on Chinese pigs, while Russian breeding resources remain

poorly studied. Therefore, the use of the described approaches for identification of selection prints in pigs, including those bred in the territory of the Russian Federation, and wild boar is a necessary condition for the effective development of pig breeding.

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