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## DOMESTICATION IS THE PROPRIETARY CASE OF EVOLUTION: ABOUT THE UNIVERSALITY OF PRINCIPLES AND ELEMENTS

(review)

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### Abstract

Accelerating changes of the biosphere in which the transformation of human activity into a geological force plays an essential role (V.I. Vernadsky, 1944) generate special attention to the management of the genetic flows of domesticated plant and animal species as the basis for existence of the modern humanity. As N.I. Vavilov noted, domestication is “an experimental evolution .... in order to manage it, a historical understanding of the evolutionary process is necessary” (N.I. Vavilov, 1987). The main mechanism of natural and artificial selection consists in the preferential reproduction of the individuals most adapted to the proposed selection conditions, that is, having reproductive success and ensuring the preservation of offspring, which underlies the “self-domestication” of some mammalian species, including humans (L. Raviv et al., 2023). Intraspecific and interspecific differentiation and cooperation for performing population reproduction tasks have been described both in animals (A.M.M. Rodrigues et al., 2023; M.A. Zeder, 2012) and in plants (R. Sharifi, C.M. Ryu, 2021). On the example of prokaryotes, it was shown that culturing under different conditions leads to a significant differentiation in cell behavior (t.e., in colony formation) in generations, and these changes are irreversible, i.e., evolution does not go backwards (“discrimination of relatives”) (O. Rendueles et al., 2015). In multicellular organisms, a significant contribution to the irreversibility of evolution is made by symbionts, the “cooperants” at the cellular (E. Rosenberg et al., 2010) and genomic (M. Ramakrishnan et al., 2021) levels. In domesticated plants and animals, most of the genome is occupied by mobile genetic elements — transposons (TE) and the products of their recombination (D. Almojil et al., 2021). Autonomous TE are descendants of exogenous viruses and sources of the main components of networks regulating gene expression profiles that affect hybridization, stress reactivity (K. Mukherjee, L.L. Moroz, 2023). Despite significant differences in the dominance of TE variants, there are certain similarities between TEs in terms of participation in basic biological processes in plants and animals, such as the formation of interphase nuclear architecture, motifs for transcription regulatory factors, etc. (Y. Qiu, C. Köhler, 2020). It should be noted that the early stages of evolution were based on the differentiation and cooperation of protobionts (RNA, proteins, lipids, carbohydrates) (Y. Shi et al., 2023), prokaryotes and eukaryotes (J. Brueckner, W.F. Martin, 2020; C. Al Jewari, S.L. Baldauf, 2023). The data obtained indicate that differentiation and cooperation are universal elements of the entire evolutionary process, in which mutualistic relationships between a multicellular organism, its microbiota, viruses and their descendants play a key role. This circumstance must be taken into account in the search for methods of managing the genetic flows of human-domesticated species in order to preserve and improve them.

Keywords: reproductive success, mutualism, domestication, transposons, microbiota, gene regulatory networks

The exceptional scientific contribution of Nikolai I. Vavilov, the outstanding scientist of the 20th century, is the theoretical foundations of selection (published in 1987) [1]. By N.I. Vavilov's definition, the selection of cultivated plants and domestic animals is essentially experimental evolution, and in order to

understand and, to a certain extent, control experimental evolution, it is necessary to historically understand the evolutionary process [1]. The term “human-controlled evolution” was suggested by N.I. Vavilov. The main goal of his work was to “learn how to control the development of the organic world”, i.e., the evolution of domestic animals and cultivated plants. In April 1932, at a meeting of the USSR Academy of Sciences, the Communist Academy and the Lenin All-Union Academy of Agricultural Sciences dedicated to the memory of C. Darwin, N.I. Vavilov said that research work with plants and animals should be permeated with the ideas of evolutionism, on the basis of which “mastery of organisms” is possible [2].

In this review, we summarized and analyzed data on the genetic and genomic mechanisms of domestication, drivers of evolution, changes in organisms due to domestication, similarities and differences between natural and artificial selection in different taxonomic groups, and the role of these events in modern anthropogenic changes of the biosphere.

Anthropocene as a factor of influence on the biosphere. The need for an evolutionary approach to identifying the mechanisms of domestication acquired particular significance at the end of the 20th century when the rapid decline in biodiversity on a global scale and the high rates of biosphere transformation due to human activity indicated that the Anthropocene, a new geological era had begun [3].

For the first time, ideas about the onset of such an era were formulated by Vladimir I. Vernadsky. In his last published article, V.I. Vernadsky wrote about a single historical process covering the entire biosphere of the planet [4]. In this article, he noted that at the beginning of the 20th century, Alexey P. Pavlov (1854-1929), a Russian and Soviet geologist, paleontologist and stratigrapher in the last years of his life, pointing to the geological role of man, wrote about the anthropogenic era experienced by humanity.

Like any era, the Anthropocene continues to evolve. Relatively intact natural ecosystems that occupied in the recent past approximately 12% of the Earth’s surface, currently account for only 1.4% [5]. Approximately 9% of the world’s population is undernourished, and this number is projected to rise to 9.8% by 2030, when more than 850 million people will face hunger [6]. Moreover, agricultural civilization has reached the limit of extensive development, occupying 38% of the earth’s surface and consuming approximately 70% of the world’s fresh water reserves with an energy consumption level of 1.2% [7].

The pace and biosphere consequences of the development of agricultural civilization have acquired particular significance in recent times. A striking example is evidence of changes in the biomass of megafauna (animal species weighing more than 10 kg) since the last major extinction event on Earth between 50,000 and 3,000 years ago, when two-thirds of mammal genera and half of species disappeared [8]. After the disaster, the global ecosystem gradually recovered, then the rate of accumulation of its biomass increased sharply (mainly due to agricultural animal species), but the increased rate of biomass accumulation is observed only for the human population [8]. The mass extinction of fauna during the Quaternary period of the Cenozoic era is hypothesized to be related to the activities of modern humans as the main driving force behind global losses of megafauna during the late Quaternary period [9]. But only with the advent of the technosphere, as a result of human intellectual activity, a global threat to his existence arose.

It is generally accepted that agricultural civilization has affected the last 12 thousand years [10], a short period compared to several billion years of biosphere evolution. However, domesticated species currently compete in mass with their wild predecessors [11]. Completed by Y.M. Bar-On et al. [11] analysis of the

distribution of biomass in different kingdoms of living species and different parts of the planet showed that out of  $\approx 550$  gigatons (Gt) C, plants accounted for  $\approx 450$  Gt C. Plants are the terrestrial dominants, animals ( $\approx 2$  Gt C) are mainly representatives of marine life, while bacteria ( $\approx 70$  Gt C) and archaea ( $\approx 7$  Gt C) predominantly occupy niches deep below the surface. Terrestrial biomass is approximately two orders of magnitude higher than marine biomass. Analysis shows that the global pyramid of marine biomass contains more consumers than producers. It also turned out that the mass of the Earth's population, which historically influences the global biomass of known taxa, including mammals, fish and plants, is an order of magnitude greater than the total mass of all wild mammals [11].

**Domestication as a phenomenon.** The transformation of the biosphere and the reduction of biodiversity have led to increasing attention to domestication as "evolution by human hands". Domestication of plants and animals is a key event in the formation of agricultural civilization. Due to the decline in biodiversity, including agricultural species [12, 13], and the global depletion of fertile soils [5], special attention has arisen to agricultural species as the basis for the existence of modern society. Apparently, this is precisely what explains the sharp increase in the number of scientific publications on the analysis of the processes and features of domestication. In 2015, M.A. Zeder [10] reports that in 2013, only 811 articles addressed issues of domestication were published in 350 journals, including 42 articles in PNAS. According to our data, in 2021 the number of such articles reached 11,077. However, there is still no clear definition of what is meant by the term "domestication," although Charles Darwin considered the domestication as accelerated evolution under artificial selection [14]. Moreover, the question remains open what are the genetic mechanisms of these events [15].

Domestication syndrome in domesticated animals and cultivated plants includes a number of characteristics that distinguish them from closely related wild species. In essence, it reflects mutualistic (symbiotic) interspecific relationships that are widespread in nature which, during domestication, are determined both by the domesticated species and by humans as the domesticator [5]. This is why the definition of domestication syndrome is still controversial even for mammalian species [16]. The only thing that does not cause controversy is that domesticated plants, animals and fungi have high phenotypic diversity compared to closely related wild species.

A general definition of domestication given by M.A. Zeder [17] emphasizes that the only difference from the mutualistic (symbiotic) relationships in the wild is the human domesticator and that the domesticated individuals must have the ability to fit into his niche [17].

The most pronounced change in domesticated animals is a decrease in brain size, primarily due to the hippocampus, hypothalamus, pituitary gland and amygdala, which regulate endocrine function and the autonomic nervous system. This affects behavioral reactions such as aggression and response to environmental stress. The dramatic decrease in the size of these regions in domestic animals may be directly related to increased thresholds for aggression and fear [17].

Changes in the brain caused by domestication occur in a mosaic manner and reflect specific adaptations to the special ecological niche of domestication. They remain stable after feralization and restoration of wild populations. Even after long time and many generations in the wild, there is no secondary evolutionary trend toward increased brain size [18]. As with other traits, the decrease in brain size in domesticated animals occurs in a species-specific manner. In pigs, brain regions that control olfactory and auditory functions are less reduced than visual or motor structures, the same is true for sheep. In rats and minks, areas of the brain that control motor functions show a greater degree of reduction than

those that control visual or olfactory functions. In caged minks, the brain parts that control motor functions reduce in size almost 11% greater than in animals in an open enclosure, and 20% greater than in wild animals. Some brain regions may increase in size during domestication, as has been reported for those involved in memory and learning in homing pigeons [17].

The same mosaic and species-specific changes occur in plants for target traits of natural and artificial selection [19, 20]. A clear example of species specificity is a comparison of mutations in the *Waxy* (*Wx*) gene, encoding starch synthase in maize and rice. In rice, selection for this mutation leads to a decrease in variability within the ~ 250 kb region of the *Wx* gene localization on chromosome 6, and the decrease in genetic variability extends to approximately 39 genes localized in this region. In maize, polygenic systems including the *ae1*, *bt2*, and *su1* genes involved in starch biosynthetic pathways are under direct artificial selection pressure [21]. Corn has a much larger genome than rice, and the localization density of structural genes is relatively low, which limits the “hitchhiking effects” therefore, only a small number of the linked genes are affected.

Interestingly, in some cases the same gene underlies parallel evolution and similar phenotypic variation in different plant species. For example, glutinous rice results from a defect of splicing donor in the *Waxy* gene, and mutations in this gene also underlie the glutinous cereal phenotypes of barley, maize, and the herbaceous perennial plant Job’s Tears [22]. Mutations of the *VIRESCENS* gene, encoding a transcription regulatory factor, alter fruit color in date and oil palms, grapes, apples, cocoa, and citrus fruits [23-25].

A similar pattern occurs in the phenotypes of domestic animals. For example, allelic variation in *KIT* tyrosine kinase receptor critical for the migration of stem cells, including melanocyte precursors, and/or *MC1R* melanocortin receptor causes color changes in goats, pigs, horses, cattle, and chickens [7].

There are also examples of multiple independent domestication of the same species through very different pathways in different regions, for example in pigs [26] and soybean varieties [27].

In general, the research results clearly indicate the coevolution of species, interactions with which underlie the formation of ethnic groups and human agrarian civilization and cultural traditions. This mutualistic cooperation is based on different genes of metabolic pathways, the cooperation of which can be specific for different varieties, breeds and species [28].

It is interesting to note that in the genome one can distinguish evolutionarily conservative genes which, as a rule, are associated with phenotypic traits characteristic of large phylogenetic taxa (order, family level), and alternative variants, the polymorphism of which is typical for the variability of smaller groups, including a wide intraspecific diversity of domesticated species [29]. E.g., the American mink has evolutionarily conserved genes that allow its assignment to aquatic and semi-aquatic mammals [30]. Genome-wide association studies (GWAS) of artificially selected semi-domesticated American minks have discovered gene polymorphisms associated with skin and fur quality. These were 10 genes for hair parameters, 163 for fur quality and 98 for skin size, 194 genes for color types, and 19 regions of chromosomes 3, 4, 5, 6, 7, 8, 9 and 10 with 33 candidate genes for fur quality, hair follicle function, and pelt size. Many genes have been identified that are associated with the hair growth and molting cycle, epidermal development, the Wnt signaling pathway (one of the intracellular pathways that regulates embryogenesis, cell differentiation, and the development of malignant tumors) and muscle development [31, 32].

The same trends are characteristic of plants. As a rule, the target genes of artificial selection exhibit increased polymorphism. Signs of domestication in

plants can be divided into three groups. The first is related to yield; these traits affect the reproduction, shape and size of plants (longer and stiffer side shoots in potatoes, non-shedded seeds in grain crops, indehiscent pods in legumes, increased fruit size in cultivated tree species). The second group of traits is associated with a reduction in chemical and physical defenses typical of closely related wild species that facilitate their dispersal into the wild (e.g., loss of bitterness in cultivated almonds, loss/reduction of awn in rice and wheat). Traits belonging to the third group relate to seed germination [33].

Accumulated data indicate that domesticated species differ from closely related wild species by increased variability of domestication targets, that is, certain sets of phenotypic traits and, accordingly, polymorphism of the genomic elements involved in their formation. Apparently, it is possible to identify a set of genomic elements that form a “subgenome” that mirrors the characteristics of the domesticator and is its main target.

Differences between artificial and natural selection. The target of selection is primarily the preferential reproduction of individuals with desirable traits. It is the conditions of reproduction, including crossing, that distinguish artificial selection from natural selection. It is not possible to obtain reliable evidence that single individuals bearing characteristics typical of domesticated forms are not found in the wild. Moreover, observations are accumulating about signs of self-domestication in a number of species, e.g., humans, bonobos, elephants. Humans as domesticators are a unique species with a complex culture and social structure, a variety of languages, and extensive use of tools. According to the human self-domestication hypothesis, this unique set of traits may be the result of an evolutionary process of self-induced domestication in which humans evolved to be less aggressive and more cooperative in order to preserve offspring. Similar processes have been described in the ancestral species of humans, the bonobo, as well as the elephant. Intraspecific self-domestication has provided distinct similarities in cognitive, behavioral, and physiological properties between humans, bonobos, and elephants, primarily aimed at the preservation of offspring [34].

In animals, there are four main forms of general changes in reproductive function during domestication, including the elimination of competition between males, the limited number of females for mating, in females, an increase in feed resources, protection from predators and a decrease in maternal stress. The genetic control of such changes involves processes associated with neural crest (NCC) development. This contributes to the formation of common features of the domestication syndrome in different taxa [35].

However, even under natural conditions, introduction into a new niche leads to an increase in behavioral activity, affecting the relationship between males and females. The dynamics of the hierarchical and behavioral structure of founder populations in new conditions can have a decisive influence on intra- and interspecific relationships, leading to their long-term changes and the formation of new behavioral responses. For founder populations that expand into a new niche separated from the parent population, the need to establish connections with unfamiliar individuals, the lack of clear territories, and initially new feed resources can change the initial hierarchical structure to which subsequent generations will adapt. The “founder sociality” hypothesis is based on observations of relatively stronger connections in the more mobile sex (males in mammals) compared to the less mobile sex (females in mammals), a relative decrease in the territories explored and increased tolerance during intra- and interspecific interactions in new conditions [36]. Natural selection favors the survival of a population through altruism (by influencing the reproductive success of the population as a whole). Reproductive value determines the realization of altruism depending on individual

differences in age, sex (males, females), and general condition; internal interactions in a group can change the reproductive value of individuals to stimulate altruism and ensure population survival [37].

Humans have domesticated genetically distant fungi for similar purposes, e.g., fermentation of foods rich in lipids and sugar, to give them an attractive appearance, smell and aromatization, and to increase the shelf life and safety of the product. Numerous independent domestication events have also occurred within the species. There is evidence of phenotypic convergence in the domestication of fungi for cheese production (*Saccharomyces cerevisiae*, *Penicillium roqueforti*, *P. camemberti* and *Geotrichum candidum*) and for the production of dried meat (*P. nalgiovense* and *P. salamii*). The convergence that followed adaptation to similar ecological niches affected colony formation (fluffiness and color), lipolysis, proteolysis, production of volatile compounds and competitiveness against food pests. Similarities have been described in the loss of genetic diversity in domesticated populations and in the degeneration of unused traits such as toxin production and sexual reproduction. Phenotypic convergence has sometimes occurred through similar mechanisms of genomic adaptation, particularly gene horizontal transfer and loss [38].

Evidence has accumulated that the sociocultural characteristics of human-created niches make a relatively greater contribution to the intraspecific differentiation of cultivated plants and domesticated animals than environmental factors [39]. That is, the main differences between natural selection and artificial selection are determined by man as a domesticator, his behavior, the characteristics of the niche he creates and the mutualistic relationships between different species he controls.

Differentiation and cooperation — from protobiopolymers to humans. It is common to associate the emergence of life on Earth with mutualism (cooperation) of protobiomolecules and competition between them with regard to stability [40].

The ancient world is represented by RNA communities with diverse catalytic properties and replicated by ribozyme-polymerases. The beginning of selection is associated with finding a balance between two extremes, a mixture of nucleotides with low order and low complexity and crystals with high order but low complexity. It is assumed that the search for such a balance results in the emergence of an evolutionary product with high order (many chains with common defined sequences), high complexity (sequence length) and, thereof, high functionality (variability), which becomes the beginning of selection [41]. Amino acids serve as catalysts, structural stabilizers, and as intermediaries in communication between RNA and lipids during protocell formation.

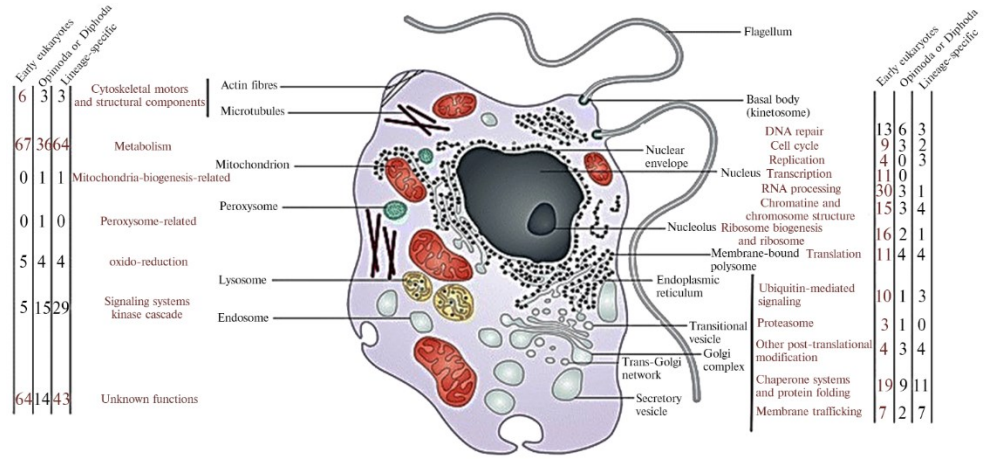
Competition between protocells is mediated by the action of the membrane-stabilizing peptide MSP, which is synthesized through the direct participation of RNA. RNA with characteristic sequences specifically binds amino acids and combines them, forming primarily dipeptides. MSP can penetrate the membrane and prevent amphiphiles (fatty acids or similar molecules) from leaving the membrane. Due to the exchange of amphiphiles between the membrane and the environment, a protocell without MSP will lose amphiphiles and shrink, while a protocell containing MSP will grow to a larger size [42].

Cooperation between archaea and proteobacteria underlies the emergence of eukaryotes and the appearance of mitochondria. On average, in eukaryotes, genes are 56% bacterial, without plastids 53%, the genes of photosynthetic eukaryote lines in which the cyanobacterial plastid ancestor contributed additional genes are 61% bacterial [43].

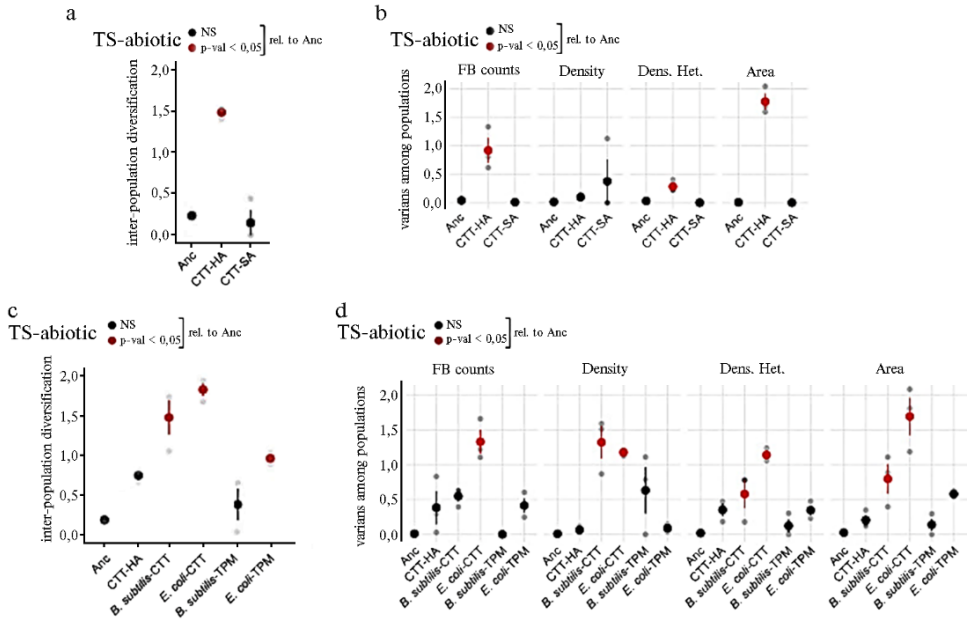
Intracellular parasites, which undergo reductive evolution as they adapt to

the nutrient-rich environment of the cells they infect, abandon bacterial metabolic control genes. This loss of adaptive genes is most pronounced in the human parasite *Encephalitozoon intestinalis*, having 86% genes of archaeal and 14% of bacterial origin. Among eukaryotes, the rice genome is the most studied, containing 67% bacterial and 33% archaeal genes. The functional dichotomy originally described for yeast, with archaeal genes involved in genetic information processing and bacterial genes involved in metabolism, is conserved across all eukaryotic supergroups [43].

The interaction of the genomes of archaea and proteobacteria has led to the emergence of a large number of chimeric genes (Fig. 1). A whole class of nuclear chimeric genes formed during endosymbiosis (S-genes, 282 families) with the subsequent evolution of eukaryotic lineages has been identified [44].



**Fig. 1. Functions of 573 S genes in a eukaryotic cell. Numbers in red correspond to functions containing important S genes in yeast [44].**



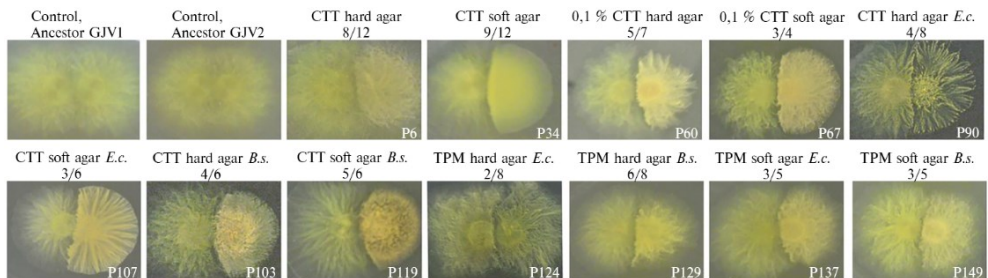
**Fig. 2. An example of morphological variability of *Myxococcus xanthus* under different treatments (TS). Populations are characterized by the number of colonies, density of colonies, heterogeneity of colonies in density, and area [46].**

Currently, the *Excavata* group is distinguished in the *Eukaryota* domain.

The phylogenetic tree branches at the base. The first major branch of eukaryotes is *Parabasalia*, followed by *Fornicata*, *Preaxostyla* and *Discoba*. The absence of aerobic mitochondria in *Parabasalia*, *Fornicata*, and *Preaxostyla* suggests that modern eukaryotes arose under anoxic conditions [45]. It is assumed that mitochondria appeared in two stages associated with two endosymbiotic events, i.e., the formation of promitochondrial and then mitochondrial structures. The first event is most likely associated with  $\gamma$ - and/or  $\delta$ -proteobacteria ( $\gamma$ -/ $\delta$ -proteo), the second event with  $\alpha$ -proteobacteria ( $\alpha$ -proteo) [45].

In prokaryotes, environmental changes lead to the emergence of new intercellular relationships, cultural and morphological properties (Fig. 2) [46]. In the study, solid agar medium (1.5%) CTT-HA or semi-solid agar (0.5%) CTT-SA was used as an abiotic factor. The biotic factor was a lawn of either *Bacillus subtilis* or *Escherichia coli* on 1.5% agar with CTT nutrient medium. Without CTT mix, *B. subtilis*-TPM and *E. coli*-TPM were grown on solid agar. With this treatment, nutrients were only available to *M. xanthus* from *B. subtilis*-TPM or *E. coli*-TPM. The range of phenotypic variability (see Fig. 2, red circles) increases on solid agar and under relative starvation (on bacterial lawns) [46].

It is important to note that when exposed to environmental factors, prokaryotes exhibit differentiation of close relatives (Fig. 3); in different organisms, so-called discrimination of relatives often occurs, while evolution is directed toward greater adaptability [47].



**Fig. 3. Examples of changes in the relationships between *Myxococcus xanthus* colonies as a result of growing on hard or soft agar, on complete medium or on lawns of *Bacillus subtilis*-TPM and *Escherichia coli*-TPM.** The first two photographs show the self-control phenotypes at colony fusion for the two ancestral variants. B.s. is *B. subtilis*; CTT is complete nutrient medium containing casiton; E.c. is *E. coli*; TPM is casiton-free medium (starvation medium) [47].

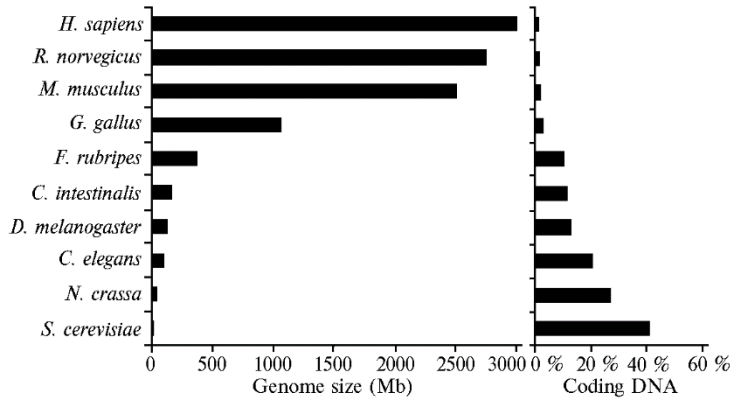
Intraspecific differentiation of closely related forms is well known, in some cases it has an obvious genetic basis (for example, between subspecies of the European rabbit). Despite the indistinguishability of the karyotypes of these two subspecies, the central (pericentromeric) region of the X chromosome is presumably involved in reproductive isolation due to disturbances in the conjugation of homologues in meiosis, which leads to limited genetic flow between subspecies. The ancestor of the domestic rabbit is the French form *Oryctolagus c. cuniculus* [48]. This limitation is as great as in Australia, where the Spanish subspecies (*O. c. algerius*) and the domestic rabbit were also introduced. The island was occupied by the Spanish subspecies and no significant appearance of crosses with the domestic rabbit was observed [49]. During intra-, as in subspecies of the European rabbit, and interspecific hybridization, the leading role is played by discrimination of chromosomes (elements of the genome of close relatives). It is usually associated with the fact that in species with sexual differentiation, mobile genetic elements (transposons) that disrupt proper meiotic divisions during the formation of gametes are accumulated in chromosomes, in particular, in the pericentromeric regions. A systematic review of studies on interspecific hybridization in mammals found that the overall incidence of negative effects (49%) was higher



than positive (13%) and neutral (38%) [50].

In plants, it has been shown that allo- and autopolyploidization lead to significant changes in gene expression profiles, activation of transposons, transcription of long non-coding RNA, microRNA, and massive structural rearrangements in genomes [51-53].

Mobile genetic elements, regulatory networks and evolution. Transposons are considered drivers of evolution and sources of various elements involved in the regulation of gene expression profiles [53-55]. In evolution, there is a consistent process of increasing genome sizes, but this increase is not accompanied by a corresponding increase in the number of protein-coding genes (Fig. 4) [56], which can be considered as an indication of the growing importance of regulatory networks. Symbiosis with transposons (mostly descendants of DNA-containing viruses and retroviruses) occupies half of the genome in higher taxa.



**Fig. 4. Eukaryotic genomes and proportion of non-coding amino acid DNA sequence from lower to higher eukaryotes.** The minimum genome size increases from simple eukaryotes (such as yeast) to complex vertebrates (such as humans). The proportion of coding DNA in larger genomes is very small, meaning that most of the genome acquired by these organisms is noncoding [56].

The abundance of transposons (TE) varies significantly in the genomes of different species. A number of studies have found that TEs serve as an important source of cis-regulatory motifs in the form of transcription regulatory factor (TF) binding sites, distal enhancer, suppressor, or segregator. A significant proportion of TFs in mammalian genomes have been derived from TEs [54, 57]. TFs generated by TEs influence three-dimensional chromatin organization and are thus involved in regulating the activity of genes that are not in close proximity. An example of this in vertebrates is the sequence to which the transcriptional regulator 11-zinc finger protein CTCF binds. CTCF is involved in the formation of loops and topologically associated domains, and is a TE derivative. It is noteworthy that TEs contribute significantly to the formation of species-specific loops in human and mouse DNA by introducing novel motifs for the TF CTCF [58]. TF CTCF binding motifs have also been identified in a number of mammalian retroviruses, in particular in the bovine leukemia provirus (BLV) [59]. The TF CTCF is involved in both the regulation of BLV transcriptional activity and the deregulation of the host three-dimensional (3D) chromatin architecture surrounding the BLV integration site. Three conserved CTCF binding motifs have been identified in BLV proviral DNA in vivo. In the BLV genome, the sequence to which CTCF binds is localized in regions of histone modifications involved in transcriptional regulation. This sequence is involved in the suppression of the activity of the 5' long terminal repeat (LTR) promoter, which leads to viral latency but at the same time promotes activity the 3' LTR promoter involved in the transcription of the corresponding long non-coding RNA (lncRNA). BLV integration disrupts the

regulation of host cell three-dimensional chromatin organization by altering the formation of chromatin loops at sites where proviral DNA integrates into the host genome. Sequences of autonomous TEs are often characterized by high variability in DNA methylation, which also affects their involvement in the regulation of gene expression.

In plants, the TF CTCF is absent, but a similar effect of TE on the spatial organization of the genome has been detected. For example, in rice and sorghum, miniature transposable elements with inverted repeats are associated with the presence of sites of attachment to the nuclear matrix and serve as “anchors” for loops [60, 61].

A gene regulatory network is a system of interactions between molecular regulators (e.g., transcription factors) and substrates (e.g., transcription factor binding sites) that control the expression of genes involved in complex biological processes [62]. There is a growing number of studies on the direct role of TEs in the evolution of gene regulatory networks and their involvement in responses to biotic and abiotic environmental factors [54, 63-65].

In plant genomes, retrotransposons with long terminal repeats (LTR retrotransposons, endogenous retroviruses ERVs) are the most common group of mobile genetic elements; they are involved in the organization of genomic architecture and in phenotypic variability. The general structure of retrotransposons and the domains responsible for the various phases of their replication are highly conserved in all eukaryotes. The chromosomes of higher plants contain two main superfamilies of LTR retrotransposons, Ty1/Copia and Ty3/Gypsy. Members of these superfamilies can increase in copy number and are often activated by various biotic and abiotic stresses due to bursts of retrotransposition. ERVs are important drivers of species variation and are characterized by great diversity in structure, size, and transposition mechanisms, making them important participants in the genome evolution [66]. In addition, ERVs influence the expression pattern of neighboring genes by being involved in the formation of small interfering RNA (siRNA) and RNA-directed DNA methylation (RdDM) [67].

TEs occupy 60-80% of the genome in maize, 29% in rice, and 17% in *Arabidopsis* [68, 69]. *Arabidopsis* (119.1 Mb) and rice (373.8 Mb) genomes are the smallest among dicotyledons and monocotyledons, respectively, and their genomes are considered reference in their classes (<https://www.ncbi.nlm.nih.gov/>), maize is has one of the longest genomes among monocots (2.3 Gb) [70].

Plant stress reactivity is closely related to transcription regulatory factors. Thus, in maize, the plant-specific AP2/ERF transcription regulatory factor superfamily includes 229 AP2/ERF genes, and their expression changes under the influence of a range of environmental stress factors. In addition, some representatives of this superfamily are involved in the sexual differentiation of plants and in the regulation of different stages of ontogeny [71]. The TF AP2/ERF superfamily, along with its involvement in responses to environmental stress factors, is directly involved in the action of plant hormones [72]. That is, regulatory systems of stress reactivity in plants are closely related to key systems of ontogeny regulation.

A comparison of the TEs contribution to the regulation of transcriptional activity was made based on their influence on the expression of nearby genes in response to stress. The relationship was investigated between the presence of TE superfamilies upstream, downstream, or within the introns of nearby genes and the differential expression of these genes under various stresses in organisms contrasting in the number of TEs in their genomes, the TE-poor *Arabidopsis thaliana* and TE-rich *Solanum lycopersicum*. It was found that the response to stress involves genes that are located close to members of various TE superfamilies, in particular SINE under proteotoxic stress, Copia and Gypsy under heat in *A. thaliana*, EPRV,

hAT during infection, Harbinger, LINE under light stress in *S. lycopersicum*. The same authors compiled a map of TE-mediated stress response regulation networks in plants based on the expression profiles of stress reactivity genes in two species that contrast in this trait. The regulatory role that TEs play in the stress response has been studied, allowing plants to more quickly adapt to new environmental conditions [73].

In the wheat genome, the sequences are approximately 85% TEs. Approximately 36% of the 70,818 genes were found to contain at least one TE insertion within a gene, mostly in three homeologs (triads). TE insertions within exons or in untranslated regions (UTRS) of one or more homeologs in a triad are associated with differences in their expression. A statistically significant correlation was found between the presence/absence of TE insertions belonging to six TE superfamilies and 17 subfamilies and the suppression of one homeologous gene. A direct relationship has been identified between the presence of TE insertions from certain superfamilies and the expression of genes associated with responses to biotic and abiotic stress. That is, TE in wheat plays an important role in controlling gene expression in a genome-specific manner [74].

TEs are widespread and diverse in conifer genomes. In some conifer species, potentially important sequence motifs have been identified in TEs that could link additional regulatory factors, contributing to the formation of a regulatory network [75]. The involvement of TEs in response to biotic factors of environmental stress in plants has been demonstrated, for example, during inoculation of coniferous seedlings with two species of fungi, which led to global changes in genomic DNA methylation and the expression of a number of TEs [76].

It is interesting to note that the same principle of cooperation between biological objects to increase plasticity in response to environmental factors is implemented differently in the animal and plant kingdoms. In animal genomes, short non-autonomous retrotransposons dominate among TEs; in plants, endogenous retroviruses dominate [54]; in animals, at least in vertebrates, the key element in the architectonics of the interphase nucleus appears to be the TF CTCF recognition motif; in plants, it is a complex set of motifs involved in protein-protein interactions [77]. The families of TEs the sequences of which are the basis for the formation of transcription regulatory factors in multicellular organisms also differ significantly [78].

One striking example of the involvement of TEs in the acquisition of new characters in animals is the formation and evolution of the mammalian placenta, associated with the activity of endogenous retroviruses, many families of which have been domesticated followed by generation of new regulatory genes or regulatory elements [79]. Of the placenta-associated TEs, two distinct groups of retroviral LTR retrotransferazones, THE1B and RLTR13D5, promoted the dispersal of hundreds of placenta-specific regulatory elements in great apes and mice, respectively.

Interestingly, TE transpositions also participated in the convergent evolution of endosperm, the nutritive tissue in flowering plants. The endosperm-specific MADS-box type I transcription factor PHERES1 (PHE1) in *Arabidopsis thaliana* interacts with two types of motifs, one of which is the MADS-box-associated canonical CARG motif, the other is a partially modified CARG motif, both enriched in DNA elements transposon Helitron [80]. Many target genes with Helitron-derived PHE1 binding motifs are highly expressed in endosperm, reflecting endosperm-specific regulation of PHE1. It is proposed that the distribution of MADS-box type I transcription factor binding motifs by Helitron contributed to the evolution of the endosperm, allowing the recruitment of critical developmental genes into the overall transcriptional network, similar to events occurred with the

participation of TEs in the formation of the mammalian placenta [81].

Taken together, the experimental data indicate that TEs are the main source of network elements to regulate gene expression profiles at the DNA level. Further, non-coding RNAs, TFs, protein-protein interactions are involved in these processes as tools for the direct action. The entire hierarchy of this regulatory system in multicellular organisms is highly sensitive to external influences and closely interacts with the microbiome, directly responding to the variability of the latter.

The microbial community associated with plants (microbiome) plays an important role in plant-plant communications. Mycorrhizal hyphae and stems of parasitic forms can mediate the signal transmission between plants without their physical contact. The use of volatile substances and root exudates and the participation of substances secreted by microbes or animals is possible. This allows the signal-generating plant to influence microbiome adaptation in the signal-receiving plant through stimulatory or competitive mechanisms [82]. Developmental plasticity allows one genome to form different phenotypes depending on external signals. This plasticity provides phenotypic ranges within which animals and plants will adapt to environmental challenges, such as climate change, and encourages an organism to create a new ecological niche by changing its environment. It is assumed that the elementary unit of evolution is the holobiont, a multicellular organism with its microbiota [83, 84].

The integration of developmental biology and ecology research into evolutionary theory has led to the emergence of a relatively new field of knowledge, the ecological evolutionary developmental biology (Eco-Evo-Devo) [85]. In general, the principles of biosphere evolution are the same, the differentiation and cooperation. Domestication is a special case of this process. Survival and adaptation are not just about the individual organism. These are concepts that span different hierarchical levels, from nucleic acids and proteins, genes and cells, to ecosystems and social structures. It becomes obvious that one of the universal paths of biological evolution is the abrupt transition from differentiation (including sexual and social differentiation) to cooperation, realized at different levels of organization of biological objects.

**DNA markers and selection.** A novel aspect in managing the genetic flows of domesticated species using DNA markers is the search for regulatory networks and their main elements the control and correction of which can significantly accelerate breeding. In different species, genome-wide sequencing has now been carried out and a search for connections between mononucleotide polymorphisms (SNPs) and variability in phenotypic traits has been performed. In particular, the largest resource to date, Zoonomy [86], has been organized on the comparative genomics of mammals. In 240 mammalian species, SNPs have been identified that may influence phenotypic traits and alter disease risk. At least 332 million nucleotides in the human genome (~ 10.7% of the genome, or more than 5 times the number of protein-coding nucleotides) and other species are unusually conserved compared to relatively rate-neutral sequences, and 4552 nucleotides are ultraconserved (almost perfectly conservative). Of the 101 million conserved SNPs, 80% are outside protein-coding exons [86].

In domesticated mammalian species, such as sheep, in most cases (~ 90%) SNPs associated with variability in economically valuable traits are localized in non-coding sequences of the genome. This leads to the assumption that the rearrangement of gene expression is the leading factor of phenotypic diversity in domesticated species [87-89] and humans due to the complexity of changing traits and the peculiarities of disease distribution [90].

Thus, it becomes obvious that the “symbiotic” relationship between

humans and agricultural plants and animals requires a certain change in the strategy and tactics of searching for genomic elements the control of which could significantly affect the controllability, speed and efficiency of breeding. Ultimately, the population genetic parameters of domesticated species result from a response to the balance of natural and artificial selection factors. This response involves key genes of metabolic pathways associated with resistance to biotic and abiotic stresses and desirable phenotypes for economically valuable traits, as well as a hierarchy of regulatory elements that is due to polymorphism of intragenomic factors, e.g., transposons, and the plasticity of the microbiota composition.

## REFERENCES

1. Vavilov N.I. *Teoreticheskie osnovy selektsii* [Theoretical foundations of selection]. Moscow, 1987 (in Russ.).
2. Revenkova A.I. *Nikolay Ivanovich Vavilov: 1887-1943* [Nikolai Ivanovich Vavilov: 1887-1943]. Moscow, 1962 (in Russ.).
3. Glazko V.I., Ivanitskaya L., Cheshko V. *Antropotsen. Filosofiya biotekhnologii. Stabil'naya adaptivnaya strategiya Homo sapiens, evolyutsionnyy risk i evolyutsionnaya semantika* [Anthropocene. Philosophy of biotechnology. Stable adaptive strategy of Homo sapiens, evolutionary risk and evolution semantics]. Moscow, 2018 (in Russ.).
4. Vernadskiy V.I. *Uspekhi sovremennoy biologii*, 1944, 18(2): 113-120 (in Russ.).
5. Guo Z., Zhang L., Li Y. Increased dependence of humans on ecosystem services and biodiversity. *PLoS ONE*, 2010, 5(10): e13113 (doi: 10.1371/journal.pone.0013113).
6. FAO, IFAD, UNICEF, WFP, WHO. *The state of food security and nutrition in the world 2020. Transforming food systems for affordable healthy diets*. FAO, Rome, 2020 (doi: 10.4060/ca9692en).
7. Andersson L., Purugganan M. Molecular genetic variation of animals and plants under domestication. *PNAS USA*, 2022, 119(30): e2122150119 (doi: 10.1073/pnas.2122150119).
8. Barnosky A.D. Megafauna biomass tradeoff as a driver of Quaternary and future extinctions. *PNAS USA*, 2008, 105(Suppl 1): 11543-11548 (doi: 10.1073/pnas.0801918105).
9. Sandom C., Faurby S., Sandel B., Svenning J.C. Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. Biol. Sci.*, 2014, 281(1787): 20133254 (doi: 10.1098/rspb.2013.3254).
10. Zeder M.A. Core questions in domestication research. *PNAS USA*, 2015, 112(11): 3191-3198 (doi: 10.1073/pnas.1501711112).
11. Bar-On Y.M., Phillips R., Milo R. The biomass distribution on Earth. *PNAS USA*, 2018, 115(25): 6506-6511 (doi: 10.1073/pnas.1711842115).
12. FAO. *The state of the world's animal genetic resources for food and agriculture*. B. Rischkowsky, D. Pilling (eds.). FAO, Rome, 2007.
13. Hazell P., Wood S. Drivers of change in global agriculture. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 2008, 363(1491): 495-515 (doi: 10.1098/rstb.2007.2166).
14. Darwin Ch. *Izmeneniya domashnikh zhivotnykh i kul'turnykh rasteniy. Tom 4* [Changes in domestic animals and cultivated plants. Volume 4]. Moscow-Leningrad, 1951 (in Russ.).
15. Purugganan M.D. What is domestication? *Trends Ecol. Evol.*, 2022, 37(8): 663-671 (doi: 10.1016/j.tree.2022.04.006).
16. Johnsson M., Henriksen R., Wright D. The neural crest cell hypothesis: no unified explanation for domestication. *Genetics*, 2021, 219(1): iyab097 (doi: 10.1093/genetics/iyab097).
17. Zeder M.A. Pathways to animal domestication. In: *Biodiversity in agriculture: domestication, evolution, and sustainability*. Cambridge University Press, Cambridge, 2012: 227-259 (doi: 10.1017/CBO9781139019514.013).
18. Kruska D.C. On the evolutionary significance of encephalization in some eutherian mammals: effects of adaptive radiation, domestication, and feralization. *Brain Behav. Evol.*, 2005, 65(2): 73-108 (doi: 10.1159/000082979).
19. Li L.F., Olsen K.M. To have and to hold: selection for seed and fruit retention during crop domestication. *Curr. Top. Dev. Biol.*, 2016, 119: 63-109 (doi: 10.1016/bs.ctdb.2016.02.002).
20. Mueller N.G., Horton E.T., Belcher M.E., Kistler L. The taming of the weed: developmental plasticity facilitated plant domestication. *PLoS ONE*, 2023, 8(4): e0284136 (doi: 10.1371/journal.pone.0284136).
21. Whitt S.R., Wilson L.M., Tenailon M.I., Gaut B.S., Buckler E.S. Genetic diversity and selection in the maize starch pathway. *PNAS USA*, 2002, 99(20): 12959-12962 (doi: 10.1073/pnas.202476999).
22. Purugganan M.D. Evolutionary insights into the nature of plant domestication. *Curr. Biol.*, 2019, 29(14): R705-R714 (doi: 10.1016/j.cub.2019.05.053).
23. Hazzouri K.M., Flowers J.M., Visser H.J., Khierallah H.S.M., Rosas U., Pham G.M., Meyer R.S., Johansen C.K., Fresquez Z.A., Masmoudi K., Haider N., El Kadri N., Idaghdour Y., Malek J.A., Thirkhill D., Markhand G.S., Krueger R.R., Zaid A., Purugganan M.D. Whole

- genome re-sequencing of date palms yields insights into diversification of a fruit tree crop. *Nat. Commun.*, 2015, 6: 8824 (doi: 10.1038/ncomms9824).
24. Singh R., Low E.T., Ooi L.C., Ong-Abdullah M., Nookiah R., Ting N.C., Marjuni M., Chan P.L., Ithnin M., Manaf M.A., Nagappan J., Chan K.L., Rosli R., Halim M.A., Azizi N., Budiman M.A., Lakey N., Bacher B., Van Brunt A., Wang C., Hogan M., He D., MacDonald J.D., Smith S.W., Ordway J.M., Martienssen R.A., Sambanthamurthi R. The oil palm VI-RESCENS gene controls fruit colour and encodes a R2R3-MYB. *Nat. Commun.*, 2014, 5: 4106 (doi: 10.1038/ncomms5106).
  25. Allan A.C., Hellens R.P., Laing W.A. MYB transcription factors that colour our fruit. *Trends Plant Sci.*, 2008, 13(3): 99-102 (doi: 10.1016/j.tplants.2007.11.012).
  26. Ottoni C., Flink L.G., Evin A., Geurg C., De Cupere B., Van Neer W., Bartosiewicz L., Linderholm A., Barnett R., Peters J., Decorte R., Waelkens M., Vanderheyden N., Ricaut F.X., Cakirlar C., Cevik O., Hoelzel A.R., Mashkour M., Karimlu A.F., Seno S.S., Daujat J., Brock F., Pinhasi R., Hongo H., Perez-Enciso M., Rasmussen M., Frantz L., Megens H.J., Crooijmans R., Groenen M., Arbuckle B., Benecke N., Vidsarsdottir U.S., Burger J., Cucchi T., Dobney K., Larson G. Pig domestication and human-mediated dispersal in western Eurasia revealed through ancient DNA and geometric morphometrics. *Mol. Biol. Evol.*, 2013, 30(4): 824-832 (doi: 10.1093/molbev/mss261).
  27. Lee G.A., Crawford G.W., Liu L., Sasaki Y., Chen X. Archaeological soybean (*Glycine max*) in East Asia: does size matter? *PLoS ONE*, 2011, 6(11): e26720 (doi: 10.1371/journal.pone.0026720).
  28. Glazko V.I. Gene and genomic levels of domestication signature (review). *Sel'skokhozyaistvennaya biologiya [Agricultural Biology]*, 2018, 53(4): 659-672 (doi: 10.15389/agrobiology.2018.4.659eng).
  29. Glazko G.V., Koonin E.V., Rogozin I.B. Molecular dating: ape bones agree with chicken entrails. *Trends Genet.*, 2005, 21(2): 89-92 (doi: 10.1016/j.tig.2004.12.006).
  30. Wang L., Zhou S., Lyu T., Shi L., Dong Y., He S., Zhang H. Comparative genome analysis reveals the genomic basis of semi-aquatic adaptation in American mink (*Neovison vison*). *Animals (Basel)*, 2022, 12(18): 2385 (doi: 10.3390/ani12182385).
  31. Valipour S., Karimi K., Do D.N., Barrett D., Sargolzaei M., Plastow G., Wang Z., Miar Y. Genome-wide detection of selection signatures for pelt quality traits and coat color using whole-genome sequencing data in American Mink. *Genes (Basel)*, 2022, 13(11): 1939 (doi: 10.3390/genes13111939).
  32. Cai Z., Villumsen T.M., Asp T., Guldbrandtsen B., Sahana G., Lund M.S. SNP markers associated with body size and pelt length in American mink (*Neovison vison*). *BMC Genet.*, 2018, 19(1): 103 (doi: 10.1186/s12863-018-0688-6).
  33. Martinez-Ainsworth N.E., Tenaillon M.I. Superheroes and masterminds of plant domestication. *Comptes Rendus Biologies*, 2016, 339(7-8): 268-273 (doi: 10.1016/j.crvi.2016.05.005).
  34. Raviv L., Jacobson S.L., Plotnik J.M., Bowman J., Lynch V., Benitez-Burraco A. Elephants as an animal model for self-domestication. *PNAS USA.*, 2023, 120(15): e2208607120 (doi: 10.1073/pnas.2208607120).
  35. Gleeson B.T., Wilson L.A.B. Shared reproductive disruption, not neural crest or tameness, explains the domestication syndrome. *Proc. Biol. Sci.*, 2023, 290(1995): 20222464 (doi: 10.1098/rspb.2022.2464).
  36. Brooks J., Yamamoto S. The founder sociality hypothesis. *Ecol. Evol.*, 2021, 11(21): 14392-14404 (doi: 10.1002/ece3.8143).
  37. Rodrigues A.M.M., Gardner A. Reproductive value and the evolution of altruism. *Trends Ecol. Evol.*, 2022, 37(4): 346-358 (doi: 10.1016/j.tree.2021.11.007).
  38. Ropars J., Giraud T. Convergence in domesticated fungi used for cheese and dry-cured meat maturation: beneficial traits, genomic mechanisms, and degeneration. *Curr. Opin. Microbiol.*, 2022, 70: 102236 (doi: 10.1016/j.mib.2022.102236).
  39. Colino-Rabanal V.J., Rodríguez-Díaz R., Blanco-Villegas M.J., Peris S.J., Lizana M. Human and ecological determinants of the spatial structure of local breed diversity. *Sci. Rep.*, 2018, 8: 6452 (doi: 10.1038/s41598-018-24641-3).
  40. El-Maarouf-Bouteau H. The seed and the metabolism regulation. *Biology (Basel)*, 2022, 11(2): 168 (doi: 10.3390/biology11020168).
  41. Mayer C. Order and complexity in the RNA world. *Life (Basel)*, 2023, 13(3): 603 (doi: 10.3390/life13030603).
  42. Shi Y., Yu C., Ma W. Towards an RNA/peptides world by the direct RNA template mechanism: the emergence of membrane-stabilizing peptides in RNA-based protocells. *Life (Basel)*, 2023, 13(2): 523 (doi: 10.3390/life13020523).
  43. Brueckner J., Martin W.F. Bacterial genes outnumber archaeal genes in eukaryotic genomes. *Genome Biol. Evol.*, 2020, 12(4): 282-292 (doi: 10.1093/gbe/evaa047).
  44. Méheust R., Bhattacharya D., Pathmanathan J.S., McInerney J.O., Lopez P., Baptiste E. Formation of chimeric genes with essential functions at the origin of eukaryotes. *BMC Biol.*, 2018, 16(1): 30 (doi: 10.1186/s12915-018-0500-0).
  45. Al Jewari C., Baldauf S.L. An excavate root for the eukaryote tree of life. *Sci. Adv.*, 2023, 9(17): eade4973 (doi: 10.1126/sciadv.ade4973).

46. La Fortezza M., Rendueles O., Keller H., Velicer G.J. Hidden paths to endless forms most wonderful: ecology latently shapes evolution of multicellular development in predatory bacteria. *Commun. Biol.*, 2022, 5(1): 977 (doi: 10.1038/s42003-022-03912-w).
47. Rendueles O., Zee P.C., Dinkelacker I., Amherd M., Wielgoss S., Velicer G.J. Rapid and wide-spread de novo evolution of kin discrimination. *PNAS USA*, 2015, 112(29): 9076-9081 (doi: 10.1073/pnas.1502251112).
48. Geraldès A., Ferrand N., Nachman M.W. Contrasting patterns of introgression at X-linked loci across the hybrid zone between subspecies of the European rabbit (*Oryctolagus cuniculus*). *Genetics*, 2006, 173: 919-933 (doi: 10.1534/genetics.105.054106).
49. Alves J.M., Carneiro M., Day J.P., Welch J.J., Duckworth J.A., Cox T.E., Letnic M., Strive T., Ferrand N., Jiggins F.M. A single introduction of wild rabbits triggered the biological invasion of Australia. *PNAS USA*, 2022, 119(35): e2122734119 (doi: 10.1073/pnas.2122734119).
50. Adavoudi R., Pilot M. Consequences of hybridization in mammals: a systematic review. *Genes (Basel)*, 2021, 13(1): 50 (doi: 10.3390/genes13010050).
51. Singh A., At V., Gupta K., Sharma S., Kumar S. Long non-coding RNA and microRNA landscape of two major domesticated cotton species. *Comput. Struct. Biotechnol. J.*, 2023, 21: 3032-3044 (doi: 10.1016/j.csbj.2023.05.011).
52. Jin S., Han Z., Hu Y., Si Z., Dai F., He L., Cheng Y., Li Y., Zhao T., Fang L., Zhang T. Structural variation (SV)-based pan-genome and GWAS reveal the impacts of SVs on the speciation and diversification of allotetraploid cottons. *Mol. Plant.*, 2023, 16(4): 678-693 (doi: 10.1016/j.molp.2023.02.004).
53. Ramakrishnan M., Satish L., Kalendar R., Narayanan M., Kandasamy S., Sharma A., Emamverdian A., Wei Q., Zhou M. The dynamism of transposon methylation for plant development and stress adaptation. *Int. J. Mol. Sci.*, 2021, 22(21): 11387 (doi: 10.3390/ijms222111387).
54. Almojil D., Bourgeois Y., Falis M., Hariyani I., Wilcox J., Boissinot S. The Structural, functional and evolutionary impact of transposable elements in eukaryotes. *Genes (Basel)*, 2021, 12(6): 918 (doi: 10.3390/genes12060918).
55. Glazko V.I., Kosovsky G.Yu., Glazko T.T. The sources of genome variability as domestication drivers (review). *Sel'skokhozyaistvennaya biologiya [Agricultural Biology]*, 2022, 57(5): 832-851 (doi: 10.15389/agrobiology.2022.5.832eng).
56. Kumar R.P., Senthilkumar R., Singh V., Mishra R.K. Repeat performance: how do genome packaging and regulation depend on simple sequence repeats? *Bioessays*, 2010, 32(2): 165-174 (doi: 10.1002/bies.200900111).
57. Jordan I.K., Rogozin I.B., Glazko G.V., Koonin E.V. Origin of a substantial fraction of human regulatory sequences from transposable elements. *Trends Genet.*, 2003, 19(2): 68-72 (doi: 10.1016/s0168-9525(02)00006-9).
58. Choudhary M.N., Friedman R.Z., Wang J.T., Jang H.S., Zhuo X., Wang T. Co-opted transposons help perpetuate conserved higher-order chromosomal structures. *Genome Biol.*, 2020, 21(1): 16 (doi: 10.1186/s13059-019-1916-8).
59. Bellefroid M., Rodari A., Galais M., Krijger P.H.L., Tjalsma S.J.D., Nestola L., Plant E., Vos E.S.M., Cristinelli S., Van Driessche B., Vanhulle C., Ait-Ammar A., Burny A., Ciuffi A., de Laat W., Van Lint C. Role of the cellular factor CTCF in the regulation of bovine leukemia virus latency and three-dimensional chromatin organization. *Nucleic Acids Res.*, 2022, 50(6): 3190-3202 (doi: 10.1093/nar/gkac107).
60. Avramova Z., Tikhonov A., Chen M., Bennetzen J.L. Matrix attachment regions and structural colinearity in the genomes of two grass species. *Nucleic Acids Res.*, 1998, 26(3): 761-767 (doi: 10.1093/nar/26.3.761).
61. Argentin J., Bolser D., Kersey P.J., Flicek P. Comparative analysis of repeat content in plant genomes, large and small. *Front. Plant Sci.*, 2023, 14: 1103035 (doi: 10.3389/fpls.2023.1103035).
62. Davidson E., Levin M. Gene regulatory networks. *PNAS USA*, 2005, 102(14): 4935 (doi: 10.1073/pnas.0502024102).
63. Chuong E.B., Elde N.C., Feschotte C. Regulatory activities of transposable elements: from conflicts to benefits. *Nat. Rev. Genet.*, 2017, 18(2): 71-86 (doi: 10.1038/nrg.2016.139).
64. Bourque G., Leong B., Vega V.B., Chen X., Lee Y.L., Srinivasan K.G., Chew J.L., Ruan Y., Wei C.L., Ng H.H., Liu E.T. Evolution of the mammalian transcription factor binding repertoire via transposable elements. *Genome Res.*, 2008, 18(11): 1752-1762 (doi: 10.1101/gr.080663.108).
65. Zattera M.L., Bruschi D.P. Transposable elements as a source of novel repetitive DNA in the eukaryote genome. *Cells*, 2022, 11(21): 3373 (doi: 10.3390/cells11213373).
66. Papolu P.K., Ramakrishnan M., Mullasserri S., Kalendar R., Wei Q., Zou L.H., Ahmad Z., Vinod K.K., Yang P., Zhou M. Retrotransposons: how the continuous evolutionary front shapes plant genomes for response to heat stress. *Front. Plant. Sci.*, 2022, 13: 1064847 (doi: 10.3389/fpls.2022.1064847).
67. Niu X., Chen L., Kato A., Ito H. Regulatory mechanism of a heat-activated retrotransposon by DDR complex in *Arabidopsis thaliana*. *Front. Plant Sci.*, 2022, 13: 1048957 (doi: 10.3389/fpls.2022.1048957).
68. Le Q.H., Wright S., Yu Z., Bureau T. Transposon diversity in *Arabidopsis thaliana*. *PNAS USA*,

- 2000, 97(13): 7376-7381 (doi: 10.1073/pnas.97.13.7376).
69. Bennetzen J.L. Transposable elements, gene creation and genome rearrangement in flowering plants. *Curr. Opin. Genet. Dev.*, 2005, 15(6): 621-627 (doi: 10.1016/j.gde.2005.09.010).
  70. Zhou S., Wei F., Nguyen J., Bechner M., Potamouis K., Goldstein S., Pape L., Mehan M.R., Churas C., Pasternak S., Forrest D.K., Wise R., Ware D., Wing R.A., Waterman M.S., Livny M., Schwartz D.C. A single molecule scaffold for the maize genome. *PLoS Genet.*, 2009, 5(11): e1000711 (doi: 10.1371/journal.pgen.1000711).
  71. Cheng C., An L., Li F., Ahmad W., Aslam M., Ul Haq M.Z., Yan Y., Ahmad R.M. Wide-range portrayal of AP2/ERF transcription factor family in maize (*Zea mays* L.) development and stress responses. *Genes (Basel)*, 2023, 14(1): 194 (doi: 10.3390/genes14010194).
  72. Xiong R., Chu Z., Peng X., Cui G., Li W., Dong L. Transcript-wide identification and expression pattern analysis to comprehend the roles of AP2/ERF genes under development and abiotic stress in *Trichosanthes kirilowii*. *BMC Plant Biol.*, 2023, 23(1): 354 (doi: 10.1186/s12870-023-04362-0).
  73. Deneweth Jyu, Van de Peer Yyu, Vermeirssen V. Nearby transposable elements impact plant stress gene regulatory networks: a meta-analysis in *A. thaliana* and *S. lycopersicum*. *BMC Genomics*, 2022, 23(1): 18 (doi: 10.1186/s12864-021-08215-8).
  74. Bariah I., Gribun L., Kashkush K. Transposable elements are associated with genome-specific gene expression in bread wheat. *Front. Plant Sci.*, 2023, 13: 1072232 (doi: 10.3389/fpls.2022.1072232).
  75. Voronova A., Rendyn-Anaya M., Ingvarsson P., Kalendar R., Ruņģis D. Comparative study of pine reference genomes reveals transposable element interconnected gene networks. *Genes (Basel)*, 2020, 11(10): 1216 (doi: 10.3390/genes11101216).
  76. Voronova A. Retrotransposon expression in response to in vitro inoculation with two fungal pathogens of Scots pine (*Pinus sylvestris* L.). *BMC Res. Notes*, 2019, 12(1): 243 (doi: 10.1186/s13104-019-4275-3).
  77. Yang T., Wang D., Tian G., Sun L., Yang M., Yin X., Xiao J., Sheng Y., Zhu D., He H., Zhou Y. Chromatin remodeling complexes regulate genome architecture in Arabidopsis. *The Plant Cell*, 2022, 34(7): 2638-2651 (doi: 10.1093/plcell/koac117).
  78. Mukherjee K., Moroz L.L. Transposon-derived transcription factors across metazoans. *Front. Cell. Dev. Biol.*, 2023, 11: 1113046 (doi: 10.3389/fcell.2023.1113046).
  79. Dunn-Fletcher C.E., Muglia L.M., Pavlicev M., Wolf G., Sun M.A., Hu Y.C., Huffman E., Tumukuntala S., Thiele K., Mukherjee A., Zoubovsky S., Zhang X., Swaggart K.A., Lamm K.Y.B., Jones H., Macfarlan T.S., Muglia L.J. Anthropoid primate-specific retroviral element THE1B controls expression of CRH in placenta and alters gestation length. *PLoS Biol.*, 2018, 16(9): e2006337 (doi: 10.1371/journal.pbio.2006337).
  80. Batista R.A., Moreno-Romero J., Qiu Y., van Boven J., Santos-González J., Figueiredo D.D., Kuhler C. The MAD5-box transcription factor PHERES1 controls imprinting in the endosperm by binding to domesticated transposons. *eLife*, 2019, 8: e50541 (doi: 10.7554/eLife.50541).
  81. Qiu Y., Kuhler C. Mobility connects: transposable elements wire new transcriptional networks by transferring transcription factor binding motifs. *Biochem. Soc. Trans.*, 2020, 48(3): 1005-1017 (doi: 10.1042/BST20190937).
  82. Sharifi R., Ryu C.M. Social networking in crop plants: wired and wireless cross-plant communications. *Plant Cell Environ.*, 2021, 44(4): 1095-1110 (doi: 10.1111/pce.13966).
  83. Rosenberg E., Sharon G., Atad I., Zilber-Rosenberg I. The evolution of animals and plants via symbiosis with microorganisms. *Environ. Microbiol. Rep.*, 2010, 2(4): 500-506 (doi: 10.1111/j.1758-2229.2010.00177.x).
  84. Guerrero R., Margulis L., Berlanga M. Symbiogenesis: the holobiont as a unit of evolution. *Int. Microbiol.*, 2013, 16(3): 133-143 (doi: 10.2436/20.1501.01.188).
  85. Feng L., Dong T., Jiang P., Yang Z., Dong A., Xie S.Q., Griffin C.H., Wu R. An ECO-EVO-DEVO genetic network model of stress response. *Hortic. Res.*, 2022, 9: uhac135 (doi: 10.1093/hr/uhac135).
  86. Christmas M.J., Kaplow I.M., Genereux D.P., Dong M.X., Hughes G.M., Li X., Sullivan P.F., Hindle A.G., Andrews G., Armstrong J.C., Bianchi M., Breit A.M., Diekhans M., Fanter C., Foley N.M., Goodman D.B., Goodman L., Keough K.C., Kirilenko B., Kowalczyk A., Lawless C., Lind A.L., Meadows J.R.S., Moreira L.R., Redlich R.W., Ryan L., Swofford R., Valenzuela A., Wagner F., Wallerman O., Brown A.R., Damas J., Fan K., Gatesy J., Grimshaw J., Johnson J., Kozyrev S.V., Lawler A.J., Marinescu V.D., Morrill K.M., Osmanski A., Paulat N.S., Phan B.N., Reilly S.K., Schaffer D.E., Steiner C., Supple M.A., Wilder A.P., Wirthlin M.E., Xue J.R., Zoonomia Consortium, Birren B.W., Gazal S., Hubley R.M., Koepfli K.P., Marques-Bonet T., Meyer W.K., Nweeia M., Sabeti P.C., Shapiro B., Smit A.F.A., Springer M.S., Teeling E.C., Weng Z., Hiller M., Levesque D.L., Lewin H.A., Murphy W.J., Navarro A., Paten B., Pollard K.S., Ray D.A., Ruf I., Ryder O.A., Pfenning A.R., Lindblad-Toh K., Karlsson E.K. Evolutionary constraint and innovation across hundreds of placental mammals. *Science*, 2023, 380(6643): eabn3943 (doi: 10.1126/science.abn3943).
  87. Davenport K.M., Massa A.T., Bhattarai S., McKay S.D., Mousel M.R., Herndon M.K., White S.N., Cockett N.E., Smith T.P.L., Murdoch B.M. Characterizing genetic regulatory elements in ovine tissues. *Front. Genet.*, 2021, 12: 628849 (doi: 10.3389/fgene.2021.628849).



88. Xiang R., Berg I.V.D., MacLeod I.M., Hayes B.J., Prowse-Wilkins C.P., Wang M., Bolormaa S., Liu Z., Rochfort S.J., Reich C.M., Mason B.A., Vander Jagt C.J., Daetwyler H.D., Lund M.S., Chamberlain A.J., Goddard M.E. Quantifying the contribution of sequence variants with regulatory and evolutionary significance to 34 bovine complex traits. *PNAS USA*, 2019, 116(39): 19398-19408 (doi: 10.1073/pnas.1904159116).
89. Naval-Sanchez M., Nguyen Q., McWilliam S., Porto-Neto L.R., Tellam R., Vuocolo T., Reverter A., Perez-Enciso M., Brauning R., Clarke S., McCulloch A., Zamani W., Naderi S., Rezaei H.R., Pompanon F., Taberlet P., Worley K.C., Gibbs R.A., Muzny D.M., Jhangiani S.N., Cockett N., Daetwyler H., Kijas J. Sheep genome functional annotation reveals proximal regulatory elements contributed to the evolution of modern breeds. *Nat. Commun.*, 2018, 9(1): 859 (doi: 10.1038/s41467-017-02809-1).
90. Albert F.W., Kruglyak L. The role of regulatory variation in complex traits and disease. *Nat. Rev. Genet.*, 2015, 16(4): 197-212 (doi: 10.1038/nrg3891).