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Advances in poultry genetics and genomics

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Introduction

This collection provides a comprehensive review of recent developments in poultry genetics and breeding, and genomics. Chapters in Part 1 cover the issues of genetic diversity, regarding domestication as well as genetics of pigmentation and morphological variants, and address the challenge of physiological constraints that poultry breeding is facing. Part 2 highlights recent research on the genetics of key traits, from production traits such as egg production to functional traits such as bone strength and their implications for breeding. Chapters in Part 3 summarise key advances in genomic selection techniques and their application in broiler and layer breeding. Part 4 chapters conclude the book by surveying emerging trends such as the use of epigenetics and genome editing in poultry breeding.

Part 1 Poultry domestication, genetics and physiology

Part 1 begins with a discussion on the origin and domestication of poultry species. Chapter 1 highlights the current theories about the pathways leading towards domestication and presents the concept of the domestication centre. The chapter also examines a number of bird species belonging to very different orders, i.e. Galliforms, Colombiforms and Ratites, the early phase of domestication, the dispersal of these species to different regions of the world, and the extent of current genetic diversity in key species.

Chapter 2 considers molecular identification of major morphological mutations in poultry species. These mutations represent landmarks in Mendelian genetics and their determinism can now be understood thanks with genomics. The chapter describes seventeen well-known phenotypes affecting the skeleton, skin appendages, feather distribution and bird growth rate, for which the underlying genetic mechanism has been identified. In most cases, the genes involved play a central role in development and their expression is modified by a change in DNA sequence, showing that most of these mutations involve regulatory changes. The molecular pathways leading to interaction between genes have also been identified in some emblematic cases.

The next chapter assesses the genetic basis for pigmentation phenotypes. There is an extensive variation in plumage colour in chicken and each breed has a characteristic plumage colour. Major progress has been made in the last 25 years with regards to understanding the developmental biology of skin and feathers in birds. Chapter 3 reviews the developmental biology of avian skin and feathers, explaining how this variation can occur through the expression of different pigments (eumelanin, pheomelanin, carotenoids and psittacofulvins) and how they are distributed across the body and within individual feathers.

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The chapter also describes how variation at 20 individual loci in the chicken genome affect skin and feather pigmentation, and the identification of genes, and in most cases the underlying mutation(s), for 13 of these loci.

The final chapter of Part 1 addresses physiological challenges in poultry breeding. The poultry industry has seen dramatic increases in body weight and growth rate but with little concomitant increase in the size, function, or performance of the heart and lung in delivery of oxygenated blood to the body. Chapter 4 discusses how these physiological limitations affect poultry breeding and production. It discusses research into quantitative trait loci (QTL) related to physiological attributes and ways of including health-related physiological traits in breeding programs. As an example, the chapter discusses research to map the genetic determinants of ascites (affecting oxygen supply), including recent successes in identifying the genetic determinants of ascites. The chapter shows how this approach could be applied to a multitude of physiological, multi-genic traits.

Part 2 Genetics and genomics of complex traits

The first chapter of Part 2 examines the genetics and genomics of meat quality traits in poultry species. Beyond meat yield, technological quality has become a key factor of competitiveness in addition to optimising sensory and nutritional quality. However, analysis of poultry meat for cutting and processing shows that its quality is still poorly controlled. Chapter 5 provides an overview of research work over the past 20 years on chicken meat quality. It focuses on the genetic control of meat quality and examines the genetic architecture of meat quality traits and candidate genes. It also reviews the input of omics studies for better meat quality characterisation.

Chapter 6 assesses the genetics and genomics of egg production traits in poultry species. The consumption of poultry eggs has been increasing globally. Increases in production and efficiency while considering both animal and human welfare are needed in order to meet this demand. The underlying genetic components that influence these traits are still largely unknown, though multiple studies are gradually identifying genetic variation that impacts these traits. The chapter describes the various traits under selection in layer breeding programs, their interactions with other economic traits, and show the improvements that have been achieved in recent decades. Information is summarized for the major poultry species, including chicken, turkey, quail and waterfowl. Methods discussed include traditional and genomic selection, as well as genome-wide association studies and identification of candidate genes for egg production in poultry. Significant progress has been obtained for egg production not only for the production of table eggs but also for the multiplication of meat birds.

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The subject of Chapter 7 is genetics and genomics of feed utilization efficiency in poultry species. Feed utilization efficiency is a trait of high economic importance in livestock production. In poultry meat and egg production, feed accounts for over 70% of total production costs. Consequently, improving feed utilization efficiency has been a major goal in the poultry industry. The efficient use of feed for livestock production also positively impacts the environment. The chapter summarizes the quantitative genetic properties (heritability and genetic correlation estimates) of feed efficiency and discusses some of its main contributing factors: basal metabolism, protein turnover, body composition, and digestive efficiency. The contribution of metabolic systems (liver, adipose tissue and skeletal muscle) and relevant genomic studies are also discussed.

Chapter 8 discusses the genetics and genomics of behavioural and welfare traits in poultry species. It reviews current research on the genetics of behavioural traits, particularly for layer hens. The focus is particularly on aggressive behaviours such as feather pecking which remain a serious problem in both cage and alternative non-cage systems. The chapter also shows the complex interactions between genetics, the environment, individuals and groups, and how a multi-level group selection approach can be used to reduce aggressive behaviour in chickens.

The next chapter examines the genetics and genomics of immunity and disease traits in poultry species. Strategies to control poultry diseases utilise selective breeding to enhance immunity and disease resistance. However, immune and disease resistance traits are difficult to measure, moderately heritable and of complex polygenic architecture. Consequently, poultry breeding programmes have only recently addressed health related traits. Chapter 9 discusses advances in genetic, genomic and functional genomic studies of immune and disease resistance in chickens and the role of the major histocompatibility complex (MHC). It reviews multi-trait selection experiments and discusses potential trade-offs between production and immunocompetence and the response to disease. The chapter also provides two genome-wide association (GWAS) studies, the first focusing on immune responses to *Salmonella* and the second on immune responses to *Campylobacter*. It concludes by highlighting how selective breeding has the potential to provide an accurate, environmentally friendly and cost-effective approach to disease control.

Part 2 of the book concludes with a chapter on the genetics and genomics of skeletal traits in poultry species. Impaired skeletal function occurs in both meat-type and layer poultry, with different aetiologies. Chapter 10 discusses quantitative genetics and genetic mapping of skeletal traits in both types of poultry. It begins with an introduction to avian bone biology which is then followed by a review of quantitative genetic studies on bone traits. The chapter also highlights genetic mapping studies of bone traits in chickens. It also

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examines how bone traits can be measured, before concluding with a section on future directions for research and resources for further information on the subject.

Part 3 Use of omics in poultry breeding

Part 3 begins with a discussion of the theory of genome wide association for QTL detection. To identify the regions on the genome that influence particular traits, GWAS assesses linkage disequilibrium (LD) between a QTL and neighbouring genetic markers. Chapter 11 examines the principles of GWAS and its use for quantitative trait loci (QTL) detection in poultry, using the analysis of egg weight in layer hens as an example. It concludes by addressing the advantages and limitations of GWAS in poultry breeding.

Chapter 12 reviews genomic selection using Bayesian methods. More recently, genomic selection (GS) has become the standard tool for genetic evaluation. One of the main challenges in the implementation of genomic selection is that the number of variants, mainly single nucleotide polymorphisms (SNPs), in the association model are far greater that the number of phenotypic records, leading to the well-known large *p*, small *n* problem. Bayesian inference provides powerful tools to circumvent this problem through the assumption of appropriate prior distributions for the unknown parameters in the association model. In this chapter, the most frequently used *prior* distributions in the implementation of genomic selection using regression models are reviewed. Bayesian strategies to accommodate non-additive effects and non-parametric approaches to predict future performance for purebred and crossbred individuals are also discussed.

Expanding on the topic of genomic selection previously highlighted in Chapter 12, Chapter 13 examines genomic selection in poultry breeding using single-step genomic best linear unbiased prediction (ssGBLUP). The chapter begins with an introduction to single-step genomic evaluation which is then followed by a discussion of genomic selection in chickens using ssGBLUP. It also addresses the implementation of genome-wide association under ssGBLUP. A section on the impact of using SNPs in genomic evaluations is also provided, as well as a section on preselection bias and crossbreeding under genomic selection. Validation, accuracies and genetic parameters in terms of genomic predictions are also discussed, before the chapter concludes with an analysis of the importance of using single-step methodology for genetic evaluation.

Chapter 14 considers the application of genomic selection in breeding commercial meat-type chickens. The chapter begins by describing the implementation stages of genomic selection in meat-type chickens (broilers), from the initial phase of testing the methodology to current developments where the technology has been consolidated into the commercial breeding

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programmes. The chapter highlights the unique characteristics of the broiler industry and discusses how these have shaped the implementation of genomic evaluations for meat-type chickens. Broiler breeders have used genomic evaluations to increase the prediction accuracy of genetic merit compared to the industry-standard of using only pedigree information for genetic evaluations. To achieve this objective, various prediction models have been applied to broiler genomic datasets. The chapter reviews these models in terms of prediction accuracy. As genomic selection is now a mature technology, the chapter offers a view on the next steps of how to further exploit the rich genomic datasets that the breeding organisations are rapidly accumulating.

The focus of Chapter 15 is the application of genomic selection in commercial egg-type populations. The important traits for commercial egg production are lifetime egg production, feed consumed per egg produced, and various internal and external egg quality traits. These traits are expressed only in females and thus the selection of males can only be done indirectly based on the performance of their female relatives, in particular sisters. Furthermore, these traits require long term data collection for most accurate information, lifetime productivity and sustainability measurements. The chapter begins by highlighting the specific advantages for selection of egg production traits. It provides a comparison between genomic and phenotypic selection and assesses analysis methods for genomic selection. The chapter summarises by providing recent reports of improvements based on genomic selection.

Chapter 16 focuses on the application of landscape genomics in poultry breeding. Landscape genomics has become an important tool to study the genetic structure of populations and to identify loci and genomic regions under natural or artificial selection. The chapter begins with an introduction to landscape genetics, which is then followed by a discussion of population and landscape genomics. It also provides a summary of the most popular methods used for the implementation of landscape genomics, specifically focusing on outlier detection methods and Environmental Association Analysis. Expanding on this, the chapter provides an assessment of using landscape genomics in both natural and livestock populations, followed by an example for the potential use of landscape genomics in the genetic improvement of backyard chickens. The chapter concludes by emphasising the advantages and limitations of using landscape genomics in the genetic improvement of livestock and commercial poultry populations.

Part 4 Emerging issues and future challenges in poultry breeding

The final part of the book begins with a discussion of breeding for small-scale poultry farming. Chapter 17 reviews the particular challenges of developing

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improved breeds of chicken for small-scale backyard poultry farming on which many smallholder families depend for a balanced diet and income. It reviews issues such as genetic resources for indigenous breeds, breeding strategies and the management strategies needed to optimize the potential of improved breeds. The chapter also discusses how new breeds can improve smallholder livelihoods.

Chapter 18 focuses on breeding for sustainability and plasticity in functional traits. It begins by examining biological functions such as reproduction, skeletal integrity and health and highlighting functional traits which are composite responses. The chapter then goes on to review phenotypic plasticity, specifically focusing on the genetic basis of plasticity and the utilization of plasticity in sustainable genetic improvement. It also assesses the genetic interrelationships between functional and performance traits. A section on resource allocation/acquisition and plasticity of the G-matrix is also included. The chapter also reviews the genetic improvement of functional traits, such as those with negative correlation with production traits and disease responses to production traits. The myths, realities and public perceptions of genetic improvement are also addressed, followed by a discussion of breeding for sustainability. Finally, the chapter concludes by providing potential resources for further information on the subject.

The next chapter considers the use of nutrigenomics in poultry breeding for sustainable production. Selection for economic phenotypic traits has significantly improved poultry productivity over the past 70 years. However, there have been a number of undesirable changes in the regulation of energy homeostasis, fat deposition (mainly in breeders), increased sensitivity to high environmental temperature and intensified incidence of metabolic disorders. Gene expression can be modulated by environmentally (diet)-induced epigenetic changes that may affect phenotypic traits in offspring. An increasing number of studies have shown that information acquired from environmental (diet) exposure may be transmitted across generations. Chapter 19 focuses on nutritional programming and transgenerational epigenetic inheritance in birds as well as the potential role of nutrigenomics in poultry breeding and selection. The chapter identifies the challenges which may help in understanding the avian epigenome and improve, in turn, the genetic selection of super parent stocks.

Chapter 20 examines the use of epigenetics in poultry breeding. Epigenetics is not commonly used in the selection of parents to breed the next generations. That is surprising as epigenetics can influence gene function, is inherited via mitosis and/or meiosis and can occur both from the female and male lines. Epigenetics has been shown to affect gene expression and can thereby play a strong role in the construction and plasticity of phenotypes in many plant and animal species, including poultry. The chapter underlines the

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key components in the poultry production chain where epigenetics can play a role. It highlights conditions influencing early-life programming by parental nutrition, thermal conditioning, and stressful events in the (grand)parents which are known to influence behaviour and welfare. The chapter concludes by suggesting that, in the analysis of phenotypic variation, one should consider both epigenetics and genetics, as epigenetics could explain a part – still to be estimated – of the variability of complex phenotypic traits.

The final chapter of the book reviews the use of genome editing in poultry breeding. Genome editing technology permits the creation of precise changes to the genome of animal species. These changes can be as small as a single base pair change in a gene or can span several megabases of DNA. Genome editing has a potential role in animal breeding as it permits the rapid and selective transfer of beneficial alleles identified in a breeding population to high-value individuals. Moreover, the removal of recessive deleterious alleles can also be used to obtain breed improvement. Chapter 21 first discusses both mammalian and avian transgenesis. It then provides an analysis of transformative technologies, specifically genome editing, which is followed by an assessment of the key challenges in genome editing for commercial poultry. The current potential applications of genome editing for poultry are also highlighted. A section on Avian Influenza Virus (AIV), a major pathogen for poultry, is also included. It concludes by stressing the importance of using genome editing as a tool to validate functional variants.

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Part 1

Poultry domestication, genetics and physiology

Chapter 1

The origin and domestication of poultry species

Michèle Tixier-Boichard, INRAE, France; and Steffen Weigend, Friedrich-Loeffler-Institut, Germany

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1 Introduction

Domestication is a complex and fascinating process that has triggered many studies and discussions, starting with mammals (Cluttonbrock, 1992). A common opinion is that domestication can be considered as a co-evolution process of humans and animals (and plants). The different approaches to study domestication were reviewed by Larson et al. (2014) who pointed out the progress expected from new techniques in archeology and genetics.

1.1 How is domestication defined?

Domestication is a continuous process of interaction between humans and the target animal or plant species that has had enormous cultural and biological impacts on our species (Larson et al., 2014). In the animal kingdom, selection by man for docility is a major feature of domestication. However, taming is limited to the fact that animals get used to living close to humans where they get food or protection, whereas domestication implies, in addition, control by

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humans of the reproduction of animals, which eventually leads to a population of animals that can be distinguished from the wild ancestor by its morphology, behavior and performance. A famous long-term experiment was set up on the domestication of the silver fox (Belyaev, 1969) which led to two divergent lines, one being friendly to humans whereas the other remained aggressive (Belyaev, 1979; Trut, 1999). Recently, in this experiment, chromosomal regions were identified that may likely explain the different behaviors between the lines (Johnson et al., 2015).

The neural crest theory has been proposed to explain the biological mechanisms involved in domestication (Wilkins et al., 2014). Selection for increased docility is likely to involve neuronal modifications, in particular regarding the hypothalamic-pituitary control of the adrenal system, which play a key role in stress and behavior. In addition, changes in the coat color take place, often toward as appearance of white spots. Taken together, these observations point toward a role for the neural crest-cell lineage that is at the origin of melanocytes as well as of neurons, which contribute to brain development and neuroendocrine functions, such as those influencing stress. Thus, Wilkins et al. (2014) suggest that a neural crest hypofunction would both decrease neuronal input into sympathetic and adrenal system and explain changes in pigmentation. Evidence in birds supporting this theory has recently been observed in guinea-fowl (Vignal et al., 2019).

From a legal viewpoint, the definition of a domestic species was proposed in the French Law for biodiversity (Law n° 2016-1087 du 8 août 2016) as follows: 'Any species which evolution process has been influenced by humans to meet their needs'. This law also gives a definition of a wild relative as 'Any animal species which can sexually reproduce with domestic ones'.

1.2 How is domestication studied?

For centuries, studies on domestication were based upon radio-dating and morphological description of ancient remains of mammals, mainly bones. Studies on ancient bones of domestic birds are less numerous than those of mammals, probably because bone remains are smaller or less well-conserved. Molecular studies of ancient tissues remain a challenge, because of the chemical modifications induced by aging of the sample, and because of the sensitivity of these studies to the contamination with DNA from modern samples. However, these studies are necessary to disentangle ancient genetic changes from those which took place in the middle-ages, for instance, as was shown for the gene encoding the thyroid-stimulating hormone receptor (*TSHR*) in chickens (Flink et al., 2014).

The first molecular tool used to study domestication is the genotyping or sequencing of mitochondrial DNA (mtDNA), and particularly its hypervariable

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region. The mtDNA is maternally transmitted and does not undergo recombination, so that the ancient migratory or introgression events can be revealed quite easily from the maternal side, but this does not tell the whole story.

The rise of genomics has significantly extended this approach, although not replacing it, by providing insight into population history through reading the whole genome. Sequencing the genome of different populations can reveal the introgression events across populations as well as the significant changes in allele frequencies within a population, suggesting an effect of past selection.

1.3 How does domestication take place: when, where and why?

As explained by Cluttonbrock (1992), domestication leads to integrating animals into the organization of a human community – animals are owned by humans and then sold, exchanged or transmitted by their owners. In this course, humans started to choose animals based on some visible traits. Recently, three pathways have been proposed to describe domestication, as reviewed by Larson and Fuller (2014): the commensal pathway does not involve any human intention whereas the other two imply a human intention, with either the prey pathway, motivated by the need to get additional food resources (as a possible reaction to overhunting), or the directed pathway, for any other intention, for instance transportation. However, these three pathways are not mutually exclusive: it is likely that domestication initially followed either a commensal or prey pathway before humans acquired the intention to influence/change an animal species for their benefit. An endless debate often takes place about the motivation for domestication, since human societies have domesticated several species of animals starting with dogs around 15 000 years ago until present time in the case of fish. Larson and Fuller (2014) considered that domestication of chicken, pigeon and common duck followed a commensal pathway whereas the prey pathway was more likely for turkeys or Muscovy ducks. Common to domesticated bird species in the early phase of domestication were various characteristics, such as the ability to forage for food, to reproduce in captivity, tamability and a social behavior that allowed them to be kept in larger populations (Sossinka, 1982, *cit. in* Crawford, 1990a). Yet, many historical records mention first cultural uses (entertainment such as cock-fighting) and religious motivations for several bird species; indeed, cock-fighting is still a common practice in some countries.

After humans observed the benefits they could obtain from domestic animals, they continued to maintain their influence on domesticated animals with more and more sophisticated technologies as time goes, as seen, for example, with the method of genomic selection currently used. Indeed, domestication is a continuous process. An important parameter to consider

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is the size of the population of animals, which has been engaged into domestication. As in any evolution or selection process, a small size of the initial population will reduce the initial gene pool and will limit the diversity of the population obtained. So, domesticated populations are generally expected to exhibit less genetic variability than their wild ancestors. This impact could be less severe if domestication took place in several sites for a given species.

The concept of domestication centre (DC) is important to understand further development of the domestic species. First, domesticated animals are expected to migrate with humans, and become more and more distant to the DC where domestication may still take place if the wild ancestors continue to evolve in its natural habitat. In that case, the wild ancestors co-exist with domestic animals, and gene flow may have continued between wild and domestic animals of a same species. This contributes to the maintenance of genetic diversity in the domestic population, as could be suggested for chickens (Berthouly et al., 2009). It also suggests that populations geographically distant from the DC will not receive this influence from the wild and will actually represent the ancient gene pool at the time they were domesticated. The gene pool that makes up these populations will likely be different from the one of domestic populations located close to the wild ancestors that may accumulate new variation. This mechanism explains the classical separation between European chicken breeds and Asian chicken breeds, except in the case of recent introduction of Asian breeds to Europe (Malomane et al., 2019).

Further differentiation of domestic birds has taken place as a result of new mutations, drift and adaptation to local conditions. In particular, plumage color mutations and morphological mutations have been accumulating, following domestication of all bird species studied until now. Two possible scenarios of differentiation can be found:

1 maintenance of a large and highly variable population, without any defined phenotypic standard, as can still be observed in village chickens of Africa, where farmers are interested to maintain a phenotypic diversity among scavenging chickens. In that case, only a large geographic distance can lead to the genetic differentiation of populations;
2 breeding according to a breed standard, when farmers and hobby breeders define a preferred morphology of the animals, in order to distinguish them from those of other areas, or other farmers; reproduction between breeds is avoided, thus creating a genetic isolation, similar to the geographic isolation at the origin of speciation. This process of breed standardization has taken place in Europe and China for chickens, since centuries. Diversity patterns of these breeds are then mainly influenced by initial size of the founder population and the management practices applied by breeders, that is, the degree of

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inbreeding within breeds and the degree of crossbreeding between breeds.

Subsequent to breed standardization, specialized lines have been developed for a high growth rate or egg production, by applying breeding goals and modern methods of selection relying on the quantitative genetics theory. These different steps are represented in Fig. 1, which shows both migration and genetic trends in domestic chickens from the DC. New breeds or lines can still be created by crossing the existing breeds or by biotechnology, with transgenesis or, more recently, genome editing. Whereas transgenesis remained in the laboratories and did not impact genetic diversity of poultry, the expectations from gene editing could have a much stronger impact.

This general scheme holds for all species of domesticated birds, which were domesticated on almost all continents and at different time periods, as will be shown in this chapter. From a phylogenetic viewpoint, the domestic birds are found across a large range of species belonging to quite different orders: Galliforms, Colombiforms, Anseriformes and Ratites. For most domestic birds, the wild ancestor species is still present in its natural habitat, which makes possible random admixture events and raises interesting research questions. Overall, this situation is a great opportunity for the preservation of gene pool of the species, although it may represent a danger for the dissemination of diseases. At least, the natural habitat of the wild species should be preserved for the sake of biodiversity.

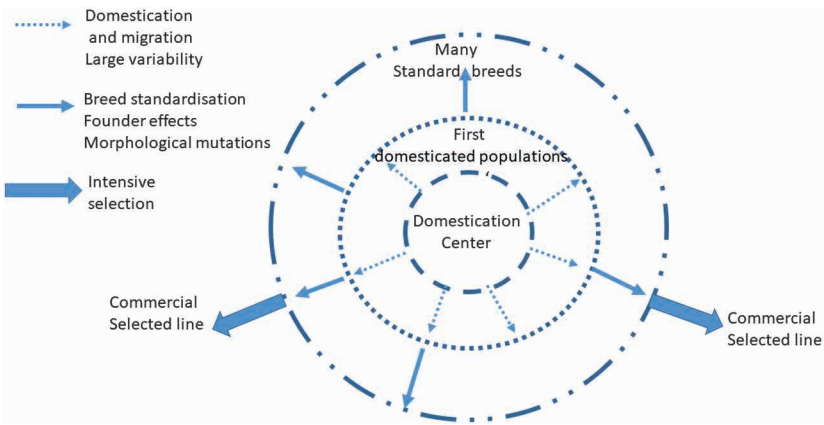

Figure 1 A schematic representation of the migration from the domestication center, followed by differentiation in breeds and commercial lines. Note that not all initial domesticated populations give rise to standard breeds, and not all standard breeds give rise to commercial lines. Each further step represents a sampling of initial genetic diversity present in the domestication center.

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