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Centenary Papers

A century of poultry genetics

M. TIXIER-BOICHARD[1], F. LEENSTRA[2], D.K FLOCK[3], P.M. HOCKING[4] and S. WEIGEND[5]*

[1]INRA, AgroParisTech, UMR1313, Animal Genetics and Integrative Biology, 78350 Jouy-en-Josas, France; [2]Wageningen UR Livestock Research, POB 65, 8200 AB, Lelystad, The Netherlands; [3]Lohmann Tierzucht GmbH, 27454 Cuxhaven, Germany; [4]The Roslin Institute and Royal (Dick) School of Veterinary Studies, University of Edinburgh, Easter Bush, Midlothian, EH25 9RG, Scotland; [5]Institute of Farm Animal Genetics, Friedrich-Loeffler-Institut, 31535 Neustadt, Germany
***Corresponding author: steffen.weigend@fli.bund.de**

The 20th Century saw an astonishing advance in our understanding of genetics and the scientific basis of the genetic improvement of farm animals. The application of genetic principles to chickens in the 1950s and 1960s led to a rapid change in the productivity and efficiency of laying hens and broiler chickens, turkeys and ducks. Subsequently, the application of increasingly powerful computers and sophisticated mathematical algorithms has increased the range of traits that could be successfully incorporated into breeding programs. Random sample tests of the performance of laying hens enjoyed a period of popularity and more recently the few remaining tests included husbandry systems in addition to strain evaluation. Characterisation of avian blood groups has led to the identification of the B21 haplotype that confers resistance to Marek's disease and to selection for this locus in commercial lines. The decade following the millennium saw the publication of the genome sequence of the chicken and the identification of millions of single nucleotide polymorphisms that, coupled with technological advances, made the application of whole genome selection practical in poultry. In parallel, the molecular basis for some Mendelian traits described a century ago is now being deciphered. Similar technologies have been applied to study genetic diversity in chickens and have provided insights into the evolution and domestication of chicken breeds. Finally, in this review, the recent development of the European Poultry Genetics Symposia coordinated by Working Group 3 'Genetics and Breeding' that was based on combining the British Poultry Breeders Round Table and AVIAGEN from West and Eastern Europe, is discussed.

Keywords: Mendelian inheritance; quantitative genetics; molecular genetics; genetic diversity; Working Group 3

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The early years: classical genetics[1]

The decade before WPSA was formed in 1912 saw the development of the basic knowledge and terminology of genetics as we know it today. The rediscovery of Mendel's experiments in 1900 by de Vries, Correns and van Tschermak demonstrated that phenotypic characters are determined by genes that segregate independently at gametogenesis and reassociate randomly at fertilisation. Two years later, Bateson and co-workers showed that Mendel's Laws applied to animals by observing that several morphological traits in chickens were inherited in a Mendelian manner: an extra toe was dominant to the normal foot, white shanks and feet were dominant to yellow, pea comb dominant to single comb and rose comb was dominant to single comb and all segregated in the expected 3:1 ratio. They reported the first instance of incomplete dominance by showing that the blue Andalusian chicken was the heterozygote from a cross between black and white parents and that segregation was in the expected 1:2:1 ratio. Partial linkage between two characters was discovered by the same group in 1905 and, together with the observation that some traits were linked to gender, led to the chromosome theory of inheritance and of linkage between genes located near each other on the same chromosome.

Sturtevant (1913) pointed out that the frequency that two genes were inherited together was a measure of the distance between them on the same chromosome and this insight eventually led to the development of linkage maps of the chromosomes (Haldane, 1919). Comprehensive chromosome maps of phenotypic characters are difficult to construct but Hutt (1949) published a genetic linkage map consisting of seven genes on the sex chromosome and 11 genes on four autosomes. Subsequently, Bitgood and Somes (1990) reviewed the literature and could map the relative positions of 17 genes on the sex chromosome, 12 on the very large chromosome 1 and a number of other genes on a further eight linkage groups.

A few of the Mendelian traits discovered in the first half of the 20th century are important in the poultry breeding industry of the 21st century. These include sex linked genes to permit identification of sex at hatching (colour sexing, barring and slow feathering genes); the dwarf gene in broiler female lines; dominant white feather colour and genes for white or yellow skin in broiler chickens. Hardy (1908) and Weinberg (1908) independently applied the concepts of Mendelian inheritance to a large population. They showed that the frequencies of the two homozygotes and the heterozygote occurred in the ratio p^2, 2pq and q^2, where p and q respectively are the frequencies of the two alleles, and remained constant from generation to generation in the absence of selection and mutation and thus initiated the study of population genetics. This simple formula is readily extended to a gene with three or more alleles, and with increasing numbers of genes and alleles, the frequency of occurrence of different traits tends to approximate to a normal bell-shaped distribution characteristic of quantitative traits such as body weight and egg production. That these traits could be determined by a large number of genes acting in a Mendelian manner was originally proposed by Bateson and Saunders in 1902, and the influence of the environment was also appreciated at this time. Punnett and Bailey (1914), in crosses between chicken breeds, showed that the variability of the second (F_2) cross was greater than in the F_1 and was consistent with the expectation that the trait depended on the effects of several genes acting cumulatively, heralding the start of quantitative genetics. These early developments were synthesised in

[1]The material in this section is covered in many good text books of genetics and as the original papers are not readily available reliance has been placed on these sources, in particular those of Hutt (1949) and Whitehouse (1969).

the seminal paper by Fisher (1918) who introduced the concept of variance components attributed to different influences and partitioned the variance of a trait into parts caused by environmental influences and genetic relationships. Fisher effectively solved the problem of how the inheritance of continuous variation for traits, such as body weight, could be attributed to Mendelian factors. This laid the foundation for the development of quantitative genetics and modern breeding methods that were subsequently collated in the classic textbook of Falconer first published in 1960 (Falconer and Mackay, 1996). Virtually all commercial poultry worldwide are hybrids of three or four lines, and the genetic basis for systems of mating and the measurement of inbreeding and relatedness was published by Wright in 1921 and 1922. These developments, established in the first decade since the founding of WPSA, set the basis for modern genetics and the later development of the poultry industry.

Developments in quantitative genetics and breeding

The theoretical basis of quantitative genetics was taught at agricultural universities from the 1920s, and several poultry science departments and government research stations initiated selection experiments to illustrate the validity of the theory (*e.g.* Lerner, 1958). Applied breeders generally followed the principle of individual testing for desired characteristics and selecting the best males and females as parents of the next generation. Gradually more geneticists with advanced degrees from reputed universities were hired by primary breeders who fine-tuned existing breeding programs. Milestones in the application of genetic theory centred around the analysis of variance between and within large populations and included

(1) Estimation of heritability to determine optimal emphasis on individual and family information to maximize the accuracy of breeding value estimation (Lush, 1937; 1947a; 1947b)
(2) Construction of selection indexes to determine total economic merit (Hazel and Lush, 1942; Hazel 1943)
(3) The time element in breeding plans to maximise progress per year instead of per generation (Dickerson and Hazel, 1944).

The theory of quantitative genetics was generally taught with reference to pure-line breeding in a given population, while breeders of laying hens were beginning to work with crossbreeding. Among dozens of universities in North America and Europe which had animal and poultry science departments, a few with outstanding contributions to progress in quantitative genetics and poultry breeding may be mentioned here: University of California in Davis (Lerner), Cornell University (Cole, Hutt, Henderson), Iowa State University (Lush, Hazel), Edinburgh (Robertson, Hill). Interestingly, several students of Lush, who worked with dairy cattle for their Ph.D. projects, were subsequently hired to optimise commercial cross-line breeding programs for laying hens.

GENETIC IMPROVEMENT OF LAYING HENS

Until about 1950, the genetic improvement of laying hen populations was generally based on individual records and family information within existing strains. White-shelled eggs were produced from White Leghorns whilst brown-shelled eggs came from a variety of heavier breeds, including Rhode Island Red, New Hampshire, Light Sussex and Barred Rock. Details of breeding plans have been treated as confidential by most breeding companies, and publications documenting the results of inbreeding and crossbreeding experiments are rare. Apparently some breeders developed superior

crosses from inbred lines, but to our knowledge no primary breeder continued inbreeding once competitive strain crosses had been established. As an alternative to the development of inbred hybrids, Comstock *et al.* (1949) proposed reciprocal recurrent selection (RRS) as a breeding plan to utilise general and specific combining ability and to maximise long-term genetic progress. Theoretical arguments favouring RRS over conventional pure-breeding were discussed at the Heterosis Conference at Iowa State University (1950) and convinced Heisdorf (1969) to introduce RRS in his layer program, while other primary breeders continued to rely on selection based on pure-line performance (Cole and Hutt, 1973). As Bell (1972) explained in a review of results from selection experiments with different species, the response to selection for combining ability depends on the initial gene frequencies in the base lines, the heritability of the traits and the number of generations. Almost 70 generations of intensive selection after Heisdorf started the RRS breeding program, the same White Leghorn strains still respond to selection. The potential importance of overdominance, an important argument in RRS theory, has never been critically analysed in commercial strain crosses. Commercial breeders today use a combination of cross-line and pure-line information to improve not only the terminal crosses, but also the elite lines.

DEVELOPMENTS IN COMPUTING

Progress in computer hardware and software has enabled primary breeders to design more sophisticated models to optimise genetic progress in an ever increasing array of traits. Earlier approaches to improve lifetime egg production by putting more weight on the latest available monthly records (Flock, 1998) were succeeded by BLUP and animal model breeding value estimation, using full-year production of previous generations (Besbes and Ducrocq, 2003). Direct selection for efficient feed conversion (residual feed intake, egg income minus feed cost) started around the middle of the 1970s at a time of high grain prices and low egg prices due to overproduction (Flock, 1998). While limited feed resources and environmental concerns call for the continued selection for efficient feed conversion, additional parameters had to be included in the breeding goal for laying hens to improve their adaptability to non-cage conditions. These include minimal feather pecking and cannibalism, nest acceptance and ranging behaviour. In the context of sustainable breeding of egg-type chickens, the focus remains on high lifetime production of saleable eggs with minimal feed cost under prevailing management conditions (Flock and Preisinger, 2002). Data collection and breeding value estimation was relatively easy between the late 1960s and 1990s, after floor management with trap nesting was replaced by single cage testing. However, the improvement of behaviour traits requires large families in cages or floor pens to expose differences in social behaviour, *i.e.* the absence of feather pecking, feather pulling and cannibalism (Muir, 1996; Ellen *et al.*, 2007; 2010).

RANDOM SAMPLE TESTS

Random sample tests (RST) for laying hens were organized in many countries to support egg producers with independent information on the performance profiles of different strains under comparable environmental conditions. This information has been useful during the second half of the 20th century and stimulated global competition among primary breeders. Several summaries of European RST were published in WPSJ (e. g. by Heil and Hartmann, 1997). German RST completed between 1975 and 1999 were analysed by Flock and Heil (2002) to document changes in the performance profiles of six white-egg and six brown-egg strains. Over the years, RST for laying hens was repeatedly on the agenda of WPSA Working Group 3 'Breeding and Genetics' (WG3). Discussion focused on questions such as the design of

tests and statistical methods for analysis of data across stations for a European summary. A conference organised by WG3 in Lelystad (NL) on Oct 13-14 1998 gathered 28 participants from testing stations, government institutions and members of WG3, in order to discuss the future of RST in Europe and underlined the interest of coordinating testing procedures and data analysis. However, only a few tests remained at the turn of the new century, and their focus had changed to management tests with different commercial strains (*e.g.* North Carolina Test with different cage density; Kitzingen Test demonstrating the effect of beak treatment under floor management conditions). Taking this situation into account, members of WG3 decided at their business meeting in 2003 to suspend activities to prepare summary reports for European testing stations until more information was available.

GENETIC IMPROVEMENT OF MEAT BIRDS

Selection of meat type chickens was comparatively unsophisticated when it started in the 1920s on the Delmarva Peninsula (Gordy, 1974). Focused on minimal age at marketable weight, breeders could generate rapid progress with mass selection for a trait with moderately high heritability, based on early measurement of live body weight in both sexes. The New York fryer market offered attractive business opportunities for pullet growers who were faced with high mortality from Marek's Disease, called 'range paralysis' at that time. An obvious benefit of rapid weight gain was the reduced risk of mortality due to a disease for which no vaccine had been developed at that time. In the 1950s, when breeders of meat-type chickens tested various breed crosses to increase growth rate and meatiness of the birds, they soon discovered a strong negative correlation between juvenile growth rate and reproductive performance. As a consequence, specialised male and female lines were developed to produce day-old chicks with the genetic potential for efficient meat production from parents with good reproductive performance. Broiler breeding became gradually more sophisticated: full sib and half sib information for body weight, conformation and liveability was used to estimate breeding values, feed consumption and carcass traits were measured on a sufficient sample of each line to evaluate the genetic potential for economic production of breast meat as accurately as possible. The increasing complexity of breeding meat-type chickens was recently reviewed by Laughlin (2007). Intensive selection continues with a focus on juvenile growth rate and feed efficiency, which can be determined in both sexes before sexual maturity and allows much higher selection intensity than is common in egg-type lines. Carcass composition is assessed in live birds with a fair degree of accuracy regarding conformation score or ultrasonic determination of breast muscle mass. Samples of sibs may be slaughtered to obtain data for family selection and to monitor correlations between live traits and the carcass traits. Carcass composition has been improved to maximise breast meat yield, and feed efficiency is evaluated relative to edible meat instead of live weight. Selection to improve soundness of legs has become more effective with the availability of specialised equipment to measure Tibial Dyschondroplasia (TD) in live animals. Challenges for future genetic improvement of broilers include the control of appetite in adult broiler breeders.

The efficiency of today's poultry would not have been possible without the application of quantitative genetics theory during the past century. The same genetic principles have also been applied to the minor poultry species, particularly to the genetic improvement of turkey and duck populations. Genetic progress is particularly beneficial because the improvement achieved through genetic selection is cumulative and permanent but may be less than expected because of genotype x environment interactions in different husbandry conditions (*e.g.* cages *vs.* range egg laying). Communication and

cooperation between academic institutions and the industry remains important to address current and future challenges. An example of this trend is the application of molecular tools and associated bioinformatics to implement genomic selection. Initially developed in cattle, where it makes possible a marked reduction in the generation interval and increase genetic progress, genomic selection is an opportunity to revise selection schemes in chickens. This technique is still at the experimental stage and is based on the use of large numbers of single nucleotide polymorphisms (SNP) to saturate the genome of individual birds with DNA markers linked to phenotypic traits. Genomic selection may be particularly useful for sex-limited traits, making early selection of males possible in laying lines, or to predict crossbred performance. The same trend towards genomics should take place in other poultry species such as ducks, turkeys and quail.

Molecular genetics

Molecular genetics started as biochemical genetics. The examples of egg white proteins and blood group B illustrate the pathway from biochemical genetics to molecular genetics before entering the era of gene mapping and finally whole-genome sequencing. Egg white proteins were initially characterized by their electrophoretic properties, with a pioneer study by Longsworth *et al.* (1940) followed by Forsythe and Foster (1950). Baker and Manwell (1962) were the first to use the terminology of 'Molecular genetics of avian proteins' and showed genetic variation at three loci: albumin A3 with quantitative variation due to a null allele, and globulins G2 and G3, showing qualitative variation with two alleles each. A survey of 10 breeds and experimental lines showed a large variation between and within breeds. In an extended survey including also two wild species, *Gallus gallus* and *Gallus sonneratii*, Baker (1968) showed a genetically controlled polymorphism for four out of the 10 proteins of egg white, and investigated the relationships between this polymorphism and breed history. No important effect of the polymorphisms of egg white proteins was found on viability or performance, but most breeds, even those being inbred, exhibited some polymorphism that suggested a selective advantage for heterozygosity. Less than 10 years after the review by Baker, chicken ovalbumin became one of the first genes to be cloned, opening the way towards molecular biology at the end of the 1970s (Humphries *et al.*, 1977). This gene was extensively used as a model to study gene structure and expression in a vertebrate, as shown by the identification of specific sequences at the exon-intron boundaries (Breathnach *et al.*, 1978). Molecular characterisation of egg proteins is still ongoing, for example, the identification of eggshell proteins (Gautron *et al.*, 2007).

Blood groups were studied very early in the history of poultry science. The review of Okada (1992) refers to a first description of erythrocyte alloantigens in chickens by Landsteiner and Miller in 1924, and a first analysis of inheritance of those antigens by Thomsen (1934). The most famous pioneers and specialists of chicken blood groups were Elwood and Ruth Briles, who developed a panel of reagents by alloimmunisation and characterised the first set of 12 erythrocyte antigens controlled by two loci, *A* and *B* (Briles *et al.*, 1950). The history of early chicken blood group investigations was related by Elwood Briles in 1984, who described his studies in different universities but also with a breeding company, DeKalb, and mentioned his friendly collaboration with Gilmour, also a pioneer of chicken blood groups (Gilmour, 1959). In contrast with egg white proteins, the adaptive value of blood group genes was observed very quickly, with a surprisingly high level of polymorphisms in most lines, even in inbred stocks (Shultz and Briles, 1953). In the early 1960s, the *B* locus was shown to be the major histocompatibility complex of the chicken (Schierman and Nordskog, 1961). Its

effect on disease resistance was extensively studied and proved to be important for susceptibility to Marek's disease, a major viral disease of chickens (Briles *et al.*, 1977). As a consequence, the B21 haplotype, associated with higher resistance in some pure lines, became the first case of marker assisted selection in poultry breeding. At the beginning of the 1980s, 29 *B* haplotypes had been differentiated across 32 experimental populations (Briles and Briles, 1982). Effects of *B* haplotypes on performance and disease resistance were extensively studied in the 1980s when many scientific papers were published, with variable results depending on lines and crossbreds. At the onset of molecular biology, the technique of Restriction Fragment Length Polymorphism (RFLP) was used to characterise further the *B*-complex and an initial molecular map was established (Guillemot *et al.*, 1988). Linkage analysis of RFLP patterns revealed the existence of another MHC region named *RFP-Y*, genetically independent from the *B*-complex (Briles *et al.,* 1993). Further studies revealed that *RFP-Y* and *B* were located on the same microchromosome but on two regions separated by a recombination hot-spot (Miller *et al.*, 1996; Fillon *et al.*, 1996). Molecular studies of the MHC genes led to a greater understanding of the evolution of this complex region (Kaufman *et al.*, 1999). A further advance was achieved for the molecular identification of *B*-haplotypes when a good correlation was found between 26 alleles of the microsatellite marker *LEI0258* and serologically defined *B*-haplotypes (Fulton *et al.*, 2006). Consequently, *B*-haplotypes can now be identified in any strain, even without a serological reagent, and a large number of new *B*-haplotypes is expected. However, despite much progress in molecular knowledge of the chicken MHC (Hosomichi *et al.*, 2008) the sequence of this region is still incomplete. Unfortunately, most of microchromosome 16, which carries the MHC as well as the nucleolar organiser, is missed by current DNA sequencing techniques.

When molecular techniques became popular in the 1980s, molecular genetics was based upon gene cloning and RFLP polymorphisms. As an example, the sex-linked dwarf gene was one of the first major genes used in poultry breeding to be identified at the molecular level when it was shown to be caused by a mutation in the GH receptor gene (Burnside *et al.*, 1991). Studies of repeated elements in the genome became popular, with the typical case of endogenous viral genes (*ALVE*) studied by several laboratories, as reviewed by Crittenden (1991). Characterisation of *ALVE* benefited from the success of the Polymerase Chain Reaction (PCR) in the 1990s with the development of locus specific diagnostic tests (Benkel, 1998). This decade would see the onset of a global approach to characterise a linkage map of the chicken genome with the development of microsatellite markers (also called VNTR standing for 'variable number of tandem repeats'), that were more numerous and more polymorphic than RFLP markers. Whereas morphological mutations and biochemical polymorphisms had been used to set up the first linkage groups of the chicken genome (Bitgood *et al.*, 1980) the development of RFLP markers made it possible to construct the first molecular map of the chicken in a cross between two inbred lines (Bumstead and Palyga, 1992). Soon afterwards, a more comprehensive map of 243 molecular markers (mostly microsatellites) organised into 32 linkage groups was produced in another cross between a red jungle fowl and a White Leghorn (Cheng *et al.,* 1995). Several laboratories participated in the mapping effort and a consensus map was finally produced in 2000 with 1889 markers, 480 of them being used as framework markers to define 50 linkage groups with a total of 3800 cM for the whole genome of 1 Gigabase (Groenen *et al.*, 2000). At the same time, cytogenetic techniques were improved with the proposal of a first standard karyotype (Ladjali-Mohammedi *et al.*, 1999) followed by the development of chromosome painting techniques and *in situ* hybridisation of BAC clones (clones of bacteria inheriting a portion of the chicken chromosome) which yielded a molecular cytogenetic

characterisation of each chicken chromosome (Masabanda *et al.*, 2004). The genetic map was extensively used to detect quantitative trait loci (QTL) by linkage analysis in dedicated designs, as reviewed by Hocking (2005), but the identification of underlying genes has had little success since then.

Only twelve years separate the RFLP map published in 1992 from the release of the first version of the whole genome sequence in 2004 (Hillier *et al.*, 2004). The resequencing of three domestic chickens (a broiler, a white-egg layer, and a Chinese local breed 'Silky') revealed a high rate of polymorphism, with about 1 SNP every 200bp, and a set of 2.8 million single nucleotide polymorphisms (SNP) was published (Wong *et al.*, 2004). Further improvements in the sequence assembly have led to good coverage of the genome, with very few errors or missing regions, apart for the smallest microchromosomes which are still absent. A high-resolution genetic map matching sequence data and former marker data has been made available recently (Groenen *et al.*, 2009). Sequence data and related information are available on-line on the Ensembl (http://www.ensembl.org/index.html) or UCSC (http://genome.ucsc.edu/) genome browsers.

Knowledge of the chicken genome has facilitated the molecular identification of genetic traits described in the period of Mendelian genetics: for example the *P* comb trait described in 1902 by Bateson was identified as a mutation in a developmental gene, *SOX5* (Wright *et al.*, 2009). Furthermore, the molecular identification of the yellow skin mutation (Hutt, 1949) has shown that it most likely originated from *Gallus sonneratii*, proving the contribution to chicken domestication of this second species in addition to *Gallus gallus* (Eriksson *et al.*, 2008). Whole genome resequencing has recently been used in chickens (Rubin *et al.*, 2010) for comparing polymorphism of the *Gallus gallus* wild ancestor genome with that of a pool of commercial lines in order to detect signatures of domestication in the genome, *i.e.* positions where allelic frequency has dramatically changed between wild jungle fowl and domestic chickens. Among the 21 domestication signatures identified, one of them involved the gene coding for the thyroid stimulating hormone receptor on chromosome 5, with a non-synonymous nucleotide change likely to have a functional consequence. The same approach successfully identified the candidate gene underlying a QTL for body weight between two divergent lines: a deletion that removes almost all the *SH3RF2* gene is associated with the allele responsible for increased growth.

Genetic diversity in chickens

Genetic diversity in chickens refers to genetic variation displayed by the numerous existing breeds and strains exhibiting a great variety of plumage colourations, morphological traits and performance levels. For thousands of years, domestic chickens have been bred for various purposes by mankind all over the world. Local populations have evolved in very distinct regions around the globe. Several events of chicken domestication are considered to have taken place in various places of Asia, mainly in China and India. A domestic gene pool arose from domestication and early breeding, from which many diversified standard breeds were developed, particularly in Europe and Asia, illustrating the degree to which man has selected for numerous characteristics in poultry. In Europe, poultry exhibitions beginning in the second half of the 19th century, had a significant influence on the development of new breeds and varieties as they encouraged breeders to pay considerable attention to specific morphological traits (Jull, 1932). In the early days of poultry breeding, emphasis was given to details of plumage colour and other Mendelian traits such as the type of comb

and earlobe colour. The varying characters which different breeds possess have served as the basis for studies on the inheritance of those traits as described above. The beginning of the 20th century was a great period in this respect. As written by R.C. Punnett in the foreword chapter of Jull's book on 'Poultry Breeding' (Jull, 1932), it was William Bateson (1861 – 1926) during his time at Cambridge, who started a series of crossing experiments in chickens. These experiments may have turned the scale, and the chicken has long been an important model organism for developmental biology (Burt, 2006). In particular, specialised genetic stocks have contributed widely to research in basic, biomedical and agricultural sciences during the last century. However, many of the more widely dispersed traditional and dual-purpose or fancy breeds have been threatened with extinction since the development of high performing commercial hybrids while the existence of experimental lines is threatened because the costs of animal husbandry are increasingly unaffordable for research institutions. WG3 has compiled an inventory, coordinated by Michele Tixier-Boichard, of experimental lines in Europe. Such an inventory will participate in a general approach to document genetic resources in poultry, but also aims at stimulating collaborations regarding the conservation and characterisation of rare or extreme genotypes. Some efforts of cryobanking have been undertaken but require further investment by public institutions (Blesbois *et al.*, 2007).

Effective management of farm animal genetic resources (FAnGR) requires comprehensive knowledge of the breeds' characteristics, including data on population size and structure, geographical distribution, the production environment, and within- and between-breed genetic diversity (Tixier-Boichard *et al.*, 2009). Describing variants of colour, morphology, behaviour, and body size and body shape has a long tradition, and detailed descriptions of the different breeds and varieties are contained in numerous books and breed standards describing phenotypic variants in poultry species. A systematic registry of genetic stocks, and mutations at the level of genes and chromosomes, has been established by Somes in the 'International Registry of Poultry Genetic Stocks'. The most recent edition was published in 1988 (Somes, 1988), and is probably the most comprehensive inventory of this kind available today. A report on poultry genetic resources in 2000 provided an update of this registry for USA, and illustrated the usefulness of these resources for research (Pisenti *et al.*, 2001). A number of databases have been established to collect information on poultry breeds, but they are not as comprehensive and are often outdated (Groeneveld *et al.*, 2010).

Early genetic diversity studies in chickens focused on morphological traits, protein variation and blood group polymorphisms (reviewed by Weigend and Romanov, 2001). Proteins showed a rather low degree of polymorphism, and hence overestimated the degree of similarity between breeds and lines, while immunogenetic markers such as blood groups encountered genotyping complications. Over the last two decades different classes of molecular markers have become available to study genetic variation (Soller *et al.*, 2006). However, since the introduction of easy-to-use PCR technologies, microsatellite markers have been widely used in diversity studies of farm animal species including chickens (Groeneveld *et al.*, 2010). Using this type of marker, an insight into the extent of diversity of a wide range of chicken breeds originating from various continents and regions has been gained in numerous studies (*e.g.* Hillel *et al.*, 2003; Granevitze *et al.*, 2007, Muchadeyi *et al.*, 2007; Mwacharo *et al.*, 2007; Berthouly *et al.*, 2008). Overall, results suggested that red jungle fowl populations and traditional unselected breeds are widely heterogeneous populations that may include a large portion of the total genetic diversity. Within commercial chickens, broiler lines were more polymorphic than layers. Among the layers, the white layers were less polymorphic than the brown layers. European breeds, of mainly standardised fancy breeds,

exhibited contrasting scenarios, ranging from extremely low genetic diversity, presumably due to positive assortative mating and small effective population size, to a rather high level of heterozygosity in some breeds that have been properly managed and kept within a reasonable size. In contrast, native populations from Africa and Asia had high genetic diversity and did not show a typical population sub-structure.

The chicken genome sequence draft and its ongoing improvement, the huge number of available single nucleotide polymophisms (SNPs) combined with highly efficient technologies of genotyping and sequencing will allow a new level of characterisation of the chicken gene pool that will aid in elucidating the biological function of genes, and hence the assessment of genetic diversity in functional traits at the molecular level. We are just at the beginning of these developments, and only a few studies have been done so far using these new tools. Genotyping approximately 3000 SNPs in commercial chicken lines and other resource populations has indicated that individual commercial breeding lines have retained only 30% of total genetic diversity (Muir *et al.*, 2008). However, it appears that modern breeding was not the primary source of this loss of alleles: the majority of the alleles were lost prior to the formation of the current commercial lines. The link between modern genomics and biodiversity will facilitate both a sustainable management of genetic diversity in poultry and its exploitation for discovering genes linked to functional diversity.

History of WPSA Working Group 3 'Breeding and Genetics'

Commercial breeding of egg-type and meat-type chickens is today concentrated in a small number of companies which maintain large populations of specialised lines to supply the world market with parent stock. For many years, geneticists from chicken breeding companies have contributed significantly to an open dialogue between the industry and academia. They initiated Poultry Breeders Roundtables in the USA and in Europe, which combined review papers, updates on knowledge and more prospective views, sometimes in other species than poultry. The first British Poultry Breeders Roundtable (BPBRT) took place in 1959 and was held each year until 1992. The US Poultry Breeders Roundtable has been taking place annually in St Louis. These roundtables operated independently from WPSA. European Working Group 3 'Breeding and Genetics' organised meetings or sessions during European poultry conferences, and supported the workshop on Genotype x Environment interactions organized by Philippe Mérat at INRA, Jouy-en-Josas in 1989. In 1993, BPBRT became the European Poultry Breeders Roundtable (EPBRT). It was decided to meet only biannually starting in Oxford, UK in 1993, followed by Foulum, Denmark in 1995. During the 1970s and 1980s when the different political systems prevented regular communication among colleagues from Eastern and Western Europe, poultry genetics meetings were organised in Eastern Europe under the name 'AVIAGEN - Current Problems in Avian Genetics'. In 1993, 'AVIAGEN' was organized in Slovakia under the chair of Jan Gavora and was, for the first time, completely open to scientists from Western Europe. In 1997, the AVIAGEN and EPBRT meetings were organised one after the other in the same week, at the same place, Pruhonice near Prague. Members of WG3 proposed that these meetings be merged into a single one, lasting two or three days. The general agreement was that WG3 should take the lead in the organisation of a single European meeting that provides an update on research in poultry genetics, and gives major importance to exchange of information and technology transfer between breeders and scientists. This biannual meeting was to be held alternately in Eastern and Western Europe, to be organised by the national branches, while the scientific programme was to

be established by WG3 members. As a result of these decisions, the First European Poultry Genetics symposium was organized in Neustadt-Mariensee, Germany, in 1999. Since then, it has been organized in Hungary (2001), Netherlands (2003), Croatia (2005), Denmark (2007), Poland (2009) and United Kingdom (2011). The symposia have stimulated the exchange of information on current research activities, encouraged the interaction between junior and senior scientists and students, and between colleagues from industry and research institutes.

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