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Review

Genetic variants for chick biology research: from breeds to mutants

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Abstract

The availability of the draft sequence of the chicken genome will undoubtedly propel an already important vertebrate research model, the domestic chicken, to a new level. This review describes aspects of chicken natural history and cross-disciplinary biological value. The diversity of extant genetic variants available to researchers is reviewed along with institutional stock locations for North America. An overview of the problem of lack of long-term stability for these resources is presented.

Keywords: Chicken; Genetics; Red Jungle Fowl; Genetic resources; Stocks crisis

1. Phylogenetics

The class Aves consists of more than 9000 species of birds inhabiting every ecological niche of the globe. Birds are warm-blooded, higher vertebrates with specialized features including adaptations for flight, feathers and in ovo embryonic development. Birds are inexorably linked to human endeavors and interests. This is true for the domestic chicken, *Gallus gallus domesticus*, having a multifaceted impact on humankind resulting from utilization for experimental biology, the global food supply, and human health (vaccine production, also impact from zoonotic diseases such as avian influenza).

The chicken belongs to the order Galliformes which includes over 200 species of small to medium-size, heavy-body birds having strong legs and toes adapted for running and scratching (food-searching) and limited long-distance flight capacity. Other well-known Galliformes include the partridge, quail, pea fowl, guinea fowl, turkey, and pheasant. Galliformes are Neognathous ('new jaw') birds, which based on morphology and biochemical classifications are as an early diverging lineage from the majority of land and water birds (Proctor and Lynch, 1993).

2. Multi-faceted contributions to research

Research utilizing the chicken has led to creation of new concepts and experimental resources valuable for different disciplines. One example of this comes from research on an economically important viral disease to the poultry industry, avian leucosis virus (ALV). The study of ALV led to development of important concepts regarding viral–host interactions in vertebrates (Crittenden, 1975), proviral insertion-mediated oncogenesis, and dysregulation of cellular oncogenes such as c-myc (see Neimann et al., 2001, 2003 and references therein). Research on ALV led to the creation of a number of important chicken genetic lines and resources (Bacon et al., 2000) including an in vitro cell line used in numerous laboratories around the world, the DT40 B-cell line (Baba et al., 1985; Buerstedde and Takeda, 1991; Arakawa et al., 2001). The 'added' value of the multi-functional nature of the chicken model is further exemplified by the recent NIH sequencing of the chicken genome. The generation of the tools essential in advance of sequencing (marker-dense linkage maps, BAC libraries, etc.) was accomplished by agricultural scientists in the US and Europe (Crittenden et al., 1993; Aerts et al. 2003; Lee et al., 2003) and financed by funding programs supportive of agricultural research (e.g. USDA in the USA, EC and BBSRC in Europe).

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3. From domestication of Red Jungle Fowl to sequencing of UCD 001

The chicken was domesticated 5000–10,000 years ago in Asia. Mitochrondrial DNA analysis indicates the domestic breeds have a monophyletic origin deriving from a single Jungle Fowl species, the Red Jungle Fowl (RJF, *G. g. gallus*) (Akishinonomiya et al., 1994; Fumihoto et al., 1996). The RJF are native to Southeast Asia and are small (~bantam size) having dark red (male) or brown (female) feathering. Females lay only one clutch of eggs per year and males exhibit an aggressive behavior and eclipse molt.

The chicken genome selected for sequencing was a RJF female from the UCD 001 inbred line. The origin of UCD 001 lies in a Malaysian-derived zoo population in Hawaii wherein during the 1940s a visiting researcher from the zoo established a research stock within the Poultry Science Department at Cornell University (Randy Cole, Cornell University, personal communication). From the Cornell RJF, a stock was established at the University of California-Berkeley and then later transferred to the University of California-Davis in the late 1950s. Matings (brother X sister) were initiated in 1956 to create an inbred line for immunology and genetic studies, later designated UCD 001 (Hans Abplanalp, University of California-Davis, personal communication). In the late 1990s, hatching eggs were sent to Michigan State University where one female was selected from which genomic resources were generated (Lee et al., 2003) and DNA from this female was used for the NIH-sequencing project (see http://genome.wustl.edu/projects/chicken/index.php).

4. Extant genetic variants: breeds, high-performance and research stocks

4.1. Breeds: locally-adapted native and standard

The dispersal of chickens from Asia followed eastern and western routes, and resulted in the development of a large number of locally adapted native breeds around the world and eventually ~100 standard breeds (with ~200 varieties) and an equal number of bantam (miniature) breeds. The result is a spectacular array of egg, plumage and structural body types with a 10-fold range in size, from 500 g to 5 kg. The main standard breed classes reflect their region of development: Europe, Mediterranean, Asian, and American. Breed standards were intentionally selected for phenotype by fancy-hobby enthusiasts and are certified by societies (e.g. American Poultry Association). A number of breed conservancy programs exist (e.g. American Livestock Breeds Conservancy http://www.albc-usa.org/, Canadian Farm Animal Genetic Resources Conservation http://www.cfagrf.com/English_Home.html) which track mid-level poultry breeds and varieties of economic or historical significance. These organizations along with government agencies (e.g. EC in Europe http://www.niwi.knaw.nl/en/oi/nod/onderzoek/OND1277942/toon and USDA in the USA http://www.ars-grin.gov/nag/, and the United Nations FAO DAD-IS Program http://dad.fao.org/) seek to conserve the alleles and allele combinations found within the various breed levels because of their value and contribution to global biodiversity and their potential to contribute to research and/or food-production applications (Delany, 2003; Hillel et al., 2003). Dating from the earliest genetic studies, it was clear that developmental and physiological mutants were often associated with specific breeds of chickens and it is likely that scientists have not yet uncovered the extent of the experimental research value resident within the standard and native breeds.

4.2. Industry Stocks

Primarily the breed stocks of the European and American classes were utilized for the development of industry stocks of layers (Single Comb White Leghorn) and broilers (White Cornish and Plymouth Rock). The industry stocks have been subject to long-term selection, some for 50 or more years (Crawford, 1990; Delany, 2000; Pisenti et al., 1999; Muir and Aggrey, 2003). Interestingly, to date there is no evidence for a ‘selection wall’ for growth production traits other than physiological constraints, e.g. heart-lung capacity (see chapters within Muir and Aggrey, 2003; Scanes et al., 2004). A combination of genetic mechanisms, e.g. high mutation and recombination rates along with combinatorial association of the large number of linkage groups of the chicken (39) may contribute to the continued plasticity of the phenotype; the chicken genome sequence will allow for testing such hypotheses.

On a collaborative basis with the companies holding breeding stock, highly selected growth and reproduction stocks are often utilized in research studies. Biomedical and developmental biology scientists are generally not as familiar with these resources. The growth and reproductive capacity of these stocks are quite unusual as compared to their normal unselected breed counterparts (Muir and Aggrey, 2003). Collaborations among applied, basic, and biomedical scientists has great potential to shift disciplinary paradigms and generate new and useful knowledge. Comparative biology and genomics allows that an agricultural research area such as skeletal strength in broilers has common ground with the biomedical research of osteoporosis and that identification of quantitative trait loci in chicken will be useful to discover important loci in humans (Jennen et al., 2002; Kerje et al., 2003).

4.3. Specialized research resources

The categories of available chicken research populations include highly inbred, congenic-inbred, long-term selected, randombred control, physiologic mutant, developmental

Table 1
Institutional locations and categories of poultry genetic research resources in North America

Country		Species			Stocks category									
Province-State (Institution, City)	Department or Laboratory	Chicken	Quail	Turkey	Inbred	Congenic	Cytogenetic	Mutant	Transgenic	Control-Random bred	Selected	Pure Breed	Gene Pool	Bloodtype-MHC
Canada														
British Columbia University of British Columbia, Vancouver	Animal Science	+	+					+			+	+		
Saskatchewan Saskatchewan, University of Saskatchewan, Saskatoon	Animal Poultry Science	+	+	+				+				+		
United States														
Alabama Auburn University, Auburn	Poultry Science	+									+		+	+
Arkansas University of Arkansas, Fayetteville	Poultry Science	+						+		+	+	+		
California University of California, Davis	Animal Science	+	+		+	+	+	+				+		
Connecticut University of Connecticut, Storrs	Agricultral Experiment Station	+						+						
Delaware University of Delaware, Newark	Animal Science	+						+						
Georgia University of Georgia, Athens	Poultry Science	+								+	+			
Illinois Northern Illinois University	Biological Sciences	+	+										+	+

(*continued on next page*)

Table 1 (*continued*)

Country		Species			Stocks category									
Province-State (Institution, City)	Department or Laboratory	Chicken	Quail	Turkey	Inbred	Congenic	Cytogenetic	Mutant	Transgenic	Control-Random bred	Selected	Pure Breed	Gene Pool	Bloodtype-MHC
University of Illinois, Urbana	Animal Science	+										+		
Indiana														
Purdue University, West Lafayette	Animal Science	+	+								+			
Iowa														
Iowa State University, Ames	Animal Science	+			+			+						
USDA, Ames	National Animal Disease Center			+						+				
Louisiana														
Louisiana State University, Baton Rouge	Poultry Science		+							+	+			
Maryland														
University of Maryland, College Park	Poultry Science		+							+				
Michigan														
USDA-ARS, East Lansing	Avian Disease and Oncology Laboratory	+			+	+			+					
Nebraska														
University of Nebraska, Lincoln	Animal Science	+	+					+		+				
New Hampshire														
University of New Hamphshire, Durham	Animal and Nutritional Sciences	+			+	+	+						+	+
New York														
Cornell University, Ithaca	Animal Science; Microbiology and Immunology	+						+		+	+			+
North Carolina														
North Carolina State University, Raleigh	Poultry Science	+		+					+	+	+	+		+

Table 1 (*continued*)

Country		Species			Stocks category									
Province-State (Institution, City)	Department or Laboratory	Chicken	Quail	Turkey	Inbred	Congenic	Cytogenetic	Mutant	Transgenic	Control-Random bred	Selected	Pure Breed	Gene Pool	Bloodtype-MHC
Ohio														
Ohio State University, Wooster	Animal Science	+	+					+		+	+			
Oregon														
Oregon State University, Corvallis	Animal Science	+											+	
Pennsylvania														
Pennsylvania State University, University Park	Poultry Science	+										+		
Virginia														
Virginia Polytechnic Institute and State University, Blacksburg	Animal and Poultry Sciences	+									+			
Wisconsin														
University of Wisconsin, Madison	Animal Science; Anatomy	+	+	+	+		+	+	+	+		+	+	

Table is adapted from Pisenti et al. (1999) with modification resulting from personal communications from the curators (to the author) and also an interim telephone survey of curator status using the list from the original report (Fulton, personal communication). Since the original survey, a number of stocks were terminated or transferred between institutions, curators retired, and a very few new stocks created. A new survey for curator status and a stocks listing is in progress (Delany, in preparation). The extent to which resources are available vary by institution; stocks or samples from stocks (e.g. fertile hatching eggs, blood, semen, etc.) may be available on a collaborative basis or cost-recovery fee basis, with many institutions now requiring a 'Material Transfer Agreement' between parties. In the USA, flock disease certificates are usually required for transfer of hatching eggs.

mutant, cytogenetic variant, pure breed, gene pool (segregating mutants or bloodtypes), bloodtype variants (MHC), and transgenic. In addition to chicken, there also exists a number of Japanese quail and turkey research lines and only a very few waterfowl or gamebird. Descriptions of poultry resources developed over the years can be found within the following, Abbott (1967), Altman and Katz (1972), Somes (1988), Crawford (1990), Abplanalp (1992), Delany and Pisenti (1998), Pisenti et al. (1999), Mozdziak et al. (2003) and Delany (2003).

Table 1 provides a listing of North American institutions holding poultry resource collections and the contact department. The list was adapted from Pisenti et al. (1999) which is available at the following url: http://www.grcp.ucdavis.edu/publications/index.htm. An update for curator status and stocks listing is in progress (Delany, in preparation) which will also either include or be linked to listings of stocks in Europe. Two European locations holding stocks include INRA (Animal Genetics Department Jouy-en-Josas Cedex, France) and the Roslin Institute (Genomics and Bioinformatics, Roslin, Midlothian, Scotland, United Kingdom).

4.4. Developmental and physiologic mutations

The phenotype and inheritance patterns of ‘structural variations’ in chicken were reported on by a number of biologists in the early 1900s (Punnett, 1923). Comb, feather and skin pigmentation variants were detailed, as well as limb variants including brachydactyl (shortened digit), syndactyly (united digits), polydactyl (extra digits), some of which were associated with particular breeds and found associated with other traits (e.g. leg feathering, scale variation). The 1st edition of F.B. Hutt’s book, ‘Genetics of the Fowl’, expanded the variant list (Hutt, 1949). A monograph by Landauer (1967) and (1973) provided a standard reference for genetic mutations and their effects. Romanoff (1972) lists and describes 20 inherited mutations causing malformations and death of the chicken embryo and 10 inherited nonlethal mutations causing malformations. Autosomal recessive and sex-linked embryonic lethal mutations were reviewed by Somes (1990) and in fact, eight chapters within Crawford (1990) highlight chicken variants and mutations (including cytogenetic variants) with another seven covering variants in other poultry species (quail, turkey, geese, pheasant). These references are of great value for their descriptions of the mutants.

Table 2 is adapted from Pisenti et al. (1999) and lists mutant lines in North America as found following a survey completed in 1998. Just a brief list of chick developmental mutants relevant to vertebrate developmental biology and human congenital malformations include the *talpid* mutants which express polydactyly with syndactyly, and lack anterior–posterior polarity (three similar, but not necessarily identical *talpid* mutations were uncovered by Cole, 1942; Abbott et al., 1960; Ede and Kelly, 1964), *wingless-2* (missing wings, possesses truncated legs), *eudiplopodia* (extra digits form dorsal to the normal digits on the foot), and *limbless* (complete absence of limbs in homozygotes) (Abbott and Pisenti, 1993; Francis-West et al., 1995; Schneider et al., 1999, see also Pisenti et al., 1999 and references therein). Physiological mutants and defects studied in chicken serve as important experimental models for human conditions (see Pisenti et al. 1999, Dodgson and Romanov, 2004). Well-studied disorders have included autoimmune vitiligo (Wang and Erf, 2004), scleroderma (Zhang and Gilliam, 2002), thyroiditis (Vasicek et al., 2001), scoliosis (Mochida et al., 1993), muscular dystrophy (Yoshizawa et al., 2003), sex-linked and autosomal dwarfing (Hutt, 1959; Agarwal et al., 1994; Tanaka et al., 1995; Ruyter-Spira et al., 1998; Cole, 2000).

5. Poultry genetic resource crisis

Pisenti et al. (1999) document the loss of literally hundred of stocks over a 15 year period (http://www.grcp.ucdavis.edu/publications/index.htm). Specialized experimental research stocks of poultry are found around the world and most of these stocks were developed at and are maintained by research institutions, academic and government, having strong agricultural science programs. An issue of enormous significance for the biological research community interested in utilizing the specialized stocks is the lack of long term stability for the majority of the chicken research resources. It is common for individual stocks and in some cases entire collections to be eliminated as poultry scientists retire, as research at agricultural institutions shift toward other areas, and as a result of the general decline in infrastructure support due to budgetary constraints at most institutions (Fulton and Delany, 2003).

The European Commission (EC) has emphasized the importance of assessment and conservation of extant genetic diversity of European chicken populations by funding the AVIANDIV project (1998–2000) a multi-laboratory collaboration to assess genetic variation within and between 52 populations including RJF, unselected morphologically variant, standard breed, selected research lines, commercial layer and broiler, and inbred lines (Hillel et al., 2003). The USDA National Animal Germplasm Program has also been working toward germplasm conservation and gaining recognition for stocks preservation. Poultry resources must be maintained as living stocks because cryopreservation of gametes and in vitro fertilization are not successful options. However, key issues for living stocks preservation have not been resolved. What has yet to be realized is the development of nationally funded initiatives to support stock centers as has been the case for other experimental systems (e.g. laboratory rodents). A plan for a system of linked national stock centers is presented within Pisenti et al. (1999).

Table 2
Listing of chicken mutant stocks in North America (from Pisenti et al., 1999)

Mutant category	Line name	Institution
Feather color	Autosomal albino	University of Wisconsin
Developmental defect		
	RC	University of British Columbia
Eye	Blind/Cataract	University of Wisconsin
	Pink-eye	University of Wisconsin
	Pop-eye	University of Wisconsin
Face/limb	Cleft primary palate/	University of California-Davis
	Scaleless	University of California-Davis
	Coloboma	University of California-Davis
	Diplopidia-1	University of California-Davis
	Diplopodia-3	University of California-Davis
	Donald-duck Beak/	University of California-Davis
	Eudiplopoda	University of California-Davis
	Limbless	University of California-Davis
	Polydactyly	University of California-Davis
	Scaless-High	University of California-Davis
	Scaless-Low	University of California-Davis
	Stumpy	University of California-Davis
	Talpid-2	University of California-Davis
	Wingless-2	University of California-Davis
	Wing-reduced	University of California-Davis
	Chondrodystrophy	University of Connecticut
	Creeper	University of Connecticut
	Diplopodia-3	University of Connecticut
	Diplopodia-5	University of Connecticut
	Limbless	University of Connecticut
	Micromelia-Abbott	University of Connecticut
	Micromelia-Hays	University of Connecticut
	Nanomelia	University of Connecticut
	Perocephaly	University of Connecticut
	Polydactyly	University of Connecticut
	Talpid-2	University of Connecticut
	Wingless-2	University of Connecticut
	Ametapodia	University of Wisconsin
	Limbless	University of Wisconsin
	Talpid-2	University of Wisconsin
	Wingless-2	University of Wisconsin
Skin–feather	Icthyosis	University of California-Davis
	Scaleless-high	University of California-Davis
	Scaless-low	University of California-Davis
	Ottawa naked	University of Connecticut
	Ptilopody	University of Connecticut
	Scaleless	University of Connecticut
	Tardy feathering	University of Wisconsin
Spine–tail	Dominant Rumplessness	University of Connecticut
	Recessive Rumpless	University of Connecticut
Immunological	Smyth Line B101	University of Arkansas
	Smyth Line B102	University of Arkansas
	Obese	Cornell University
Neurological	UNL paroxysm	University of Nebraska
	Epileptiform seizures	Unviersity of Saskatchewan
	Pirouette	University of Wisconsin
Physiologic	Sex-linked dwarf	Cornell University
	Low-score normal	Ohio State University
	Muscular dystrophy	Ohio State University
	Muscular dystrophy	University of California-Davis
	Crooked-neck dwarf	University of California-Davis
	Crooked-neck dwarf	University of Connecticut
	Musclar dystrophy	University of Connecticut
	Athens–Canadian dwarf	University of Georgia
Reproductive	Sd Line	University of Arkansas
	Double oviduct	University of Wisconsin
	Restricted ovulator	University of Wisconsin

List is adapted from Pisenti et al. (1999), see citation for full listing and stock descriptions plus Japanese quail and turkey resources. Many stocks have been dropped or transferred; thus for status, contact the institution listed and department (see Table 1). Status of University of Wisconsin stocks is highly tenuous, many are slated for elimination and transfer (Mark Cook, personal communication).

It is essential that the entire chick biology research community collaborate to promote funding initiatives to achieve long-term stability for the specialized chicken genetic resources. Novel opportunities now exist from the available chicken genome sequence for future research to better understand vertebrate development, physiology and disease. The extant chicken genetic resources are valuable and irreplaceable entities for such efforts.

References

Abbott, U.K., 1967. Avian developmental genetics. In: Will, F.W., Kessels, N.K. (Eds.), Methods in Developmental Biology. Crowell Co, New York, pp. 12–52.

Abbott, U.K., Pisenti, J.M., 1993. Making the connection: exploring classical concepts in normal and abnormal limb development using contemporary approaches. Prog. Clin. Biol. Res. 383A, 99–112.

Abbott, U., Taylor, L.W., Abplanalp, H., 1960. Studies with talpid^2, an embryonic lethal of the fowl. J. Heredity 51, 195–202.

Abplanalp, H., 1992. Inbred lines as genetic resources of chickens. Poultry Sci. Rev. 4, 29–39.

Aerts, J., Crooijmans, R., Cornelissen, S., Hemmatian, K., Veenendaal, T., Jaadar, A., van der Poel, J., Fillon, V., Vignal, A., Groenen, M., 2002. Integration of chicken genomic resources to enable whole-genome sequencing. Cytogenet. Genome Res. 102, 297–303.

Agarwal, S.K., Cogburn, L.A., Burnside, J., 1994. Dysfunctional growth hormone receptor in a strain of sex-linked dwarf chicken: evidence for a mutation in the intracellular domain. J. Endocrinol. 142, 427–434.

Akishinonomiya, F., Miyake, T., Sumit, S., Takada, M., Ohno, S., Kondo, N., 1994. One subspecies of the red junglefowl (*Gallus gallus gallus*) suffices as the matriarchic ancestor of all domestic breeds. PNAS (USA) 91, 12505–12509.

Altman, P.L., Katz, D.D. (Eds.), 1972. Chicken. In Inbred and Genetically Defined Strains of Laboratory Animals. Part 2, III. FASEB, Bethesda MD, pp. 607–684.

Arakawa, H., Lodygin, D., Buerstedde, J.M., 2001. Mutant loxP vectors for selectable marker recycle and conditional knock-outs. BMC Biotechnol. 1, 7.

Baba, T.W., Giroir, B.P., Humphries, E.H., 1985. Cell lines derived from avian lymphomas exhibit two distinct phenotypes. Virology 144, 139–151.

Bacon, L.D., Hunt, H.D., Cheng, H.H., 2000. A review of the development of chicken lines to resolve genes determining resistance to diseases. Poultry Sci. 79, 1082–1093.

Buerstedde, J.M., Takeda, S., 1991. Increased ratio of targeted to random integration after transfection of chicken B cell lines. Cell 67, 179–188.

Cole, R.K., 1942. The "talpid" lethal in the domestic fowl. J. Heredity 33, 82–86.

Cole, R.K., 2000. An autosomal dwarfism in the domestic fowl. Poultry Sci. 79, 1507–1516.

Crawford, R.D. (Ed.), 1990. Poultry, Breeding and Genetics. Elsevier Publishers, BV, Amsterdam, p. 1123.

Crittenden, L.B., 1975. Two levels of genetic resistance to lymphoid leucosis. Avian Dis. 19, 281–292.

Crittenden, L.B., Provencher, L., Santangelo, L., Levin, I., Abplanalp, H., Briles, R.W., Briles, W.E., Dodgson, J.B., 1993. Characterization of a red jungle fowl by white leghorn backcross reference population for molecular mapping of the chicken genome. Poultry Sci. 72, 334–348.

Delany, M.E., 2000. Importance of biodiversity preservation for research and industry. Proceedings of the XXI World's Poultry Congress, Montreal, Canada..

Delany, M.E., 2003. Genetic diversity and conservation of poultry. In: Muir, W.M., Aggrey, S.E. (Eds.), Poultry Genetics, Breeding and Biotechnology. CABI Publishing, Wallingford, UK, p. 706.

Delany, M.E., Pisenti, J.M., 1998. Conservation of poultry genetic research resources: Consideration of the past, present and future. Poultry Avian Biol. Rev. 9, 25–42.

Dodgson, J.B., Romanov, M.N., 2004. Use of chicken models for the analysis of human disease. In: Dracopoli, N.C., Haines, J.L., Korf, B.R., Moir, D.T., Morton, C.C., Seidman, C.E., Seidman, J.G., Smith, D.R. (Eds.), Current protocols in Human Genetics. John Wiley & Sons, Hoboken, NJ, in press.

Ede, D.A., Kelly, W.A., 1964. Developmental abnormalities in the head region of the talpid^3 mutant of the fowl. J. Embryol. Exp. Morphol. 12, 161–182.

Francis-West, P.H., Robertson, K.E., Ede, D.A., Rodriguez, C., Izpisua-Belmonte, J.C., Houston, B., Burt, D.W., Gribbin, C., Brickell, P.M., Tickle, C., 1995. Expression of genes encoding bone morphogenetic proteins and sonic hedgehog in talpid (ta3) limb buds: their relationships in the signaling cascade involved in limb patterning. Dev. Dyn. 203, 187–197.

Fulton, J.E., Delany, M.E., 2003. Poultry genetic resources—operation rescue needed. Science 300, 1667–1668.

Fumihoto, A., Miyaka, T., Takada, M., Shingu, R., Endo, E., Gojobori, T., Kondo, N., Ohno, S., 1996. Monophyletic origin and unique dispersal pattern of domestic fowl. PNAS USA 93, 6792–6795.

Hillel, J., Groenen, M.A.M., Tixier-Boichard, M., Korol, A.B., David, L., Kirzhner, V.M., Burke, T., Barre-Dirie, A., Crooijmans, R.P.M.A., Elo, K., Feldman, M.W., Freidlin, P.J., Maki-Tanila, A., Oortwijn, M., Thomson, P., Vignal, A., Wimmers, K., Weigend, S., 2003. Biodiversity of 52 chicken populations assessed by microsatellite typing of DNA pools. Genet. Sel Evol. 35, 533–557.

Hutt, F.B., 1949. Genetics of the fowl. McGraw-Hill Book Company, Inc, New York, 590 pp.

Hutt, F.B., 1959. Sex-linked dwarfism in the fowl. J. Heredity 50, 209–221.

Jennen, D.G.J., Crooijmans, R.P.M.A., Kamps, B., Acar, R., Veenendall, A., van der Poel, J.J., Groenen, M.A.M., 2002. A comparative map of chicken chromosome 24 and human chromosome 11. Animal Genet. 33, 205–210.

Kerje, S., Carlborg, Ö., Jacobbson, L., Schütz, K., Hartmann, C., Jensen, P., Andersson, L., 2003. The twofold difference in adult size between red junglefowl and White Leghorn chickens is largely explained by a limited number of QTLs. Animal Genet. 34, 264–274.

Landauer, W., 1967. The hatchability of chicken eggs as influenced by environment and heredity. Storrs Agr. Exp. Sta., Monogr., 1.

Landauer, W., 1973. The hatchability of chicken eggs as influenced by environment and heredity. Storrs Agr. Exp. Sta., Monogr. (Suppl. 1).

Lee, M.-K., Ren, C.W., Yan, B., Cox, B., Zhang, H.-B., Romanov, M.N., Sizemore, F.G., Suchyta, S.P., Peters, E., Dodgson, J.B., 2003. Construction and characterization of three BAC libraries for analysis of the chicken genome. Animal Genet. 32, 151.

Mochida, J., Benson, D.R., Abbott, U., Rucker, R.B., 1993. Neuromorphometric changes in the ventral spine roots in a scoliotic animal. Spine 18, 350–355.

Mozdziak, P.E., Borwornpinyo, S., McCoy, D.W., Petitte, J.N., 2003. Development of transgenic chickens expressing bacterial beta-galactosidase. Dev. Dyn. 226, 439–445.

Muir, W.M., Aggrey, S.E. (Eds.), 2003. Poultry Genetics. Breeding and Biotechnology. CABI Publishing, Wallingford, UK, p. 706.

Neimann, P.E., Ruddell, A., Jasoni, C., Loring, G., Thomas, S.J., Brandvold, K.A., Lee, R.M., Burnside, J., Delrow, J., 2001. Analysis of gene expression during myc oncogene-induced lymphomagenesis in the bursa of Fabricius. PNAS USA 98, 6378–6383.

Neiman, P.E., Grbiç, J.J., Polony, T.S., Kimmel, R., Bowers, S.J., Delrow, J., Beemon, K.L., 2003. Functional genomic analysis reveals neoplastic phenotypes associated with c-myb mutation in the bursa of Fabricius. Oncogene 22, 1073–1086.

Pisenti, J.M., Delany M.E., Taylor, R.L. Jr., Abbott U.K., Abplanalp H., Arthur J.A., Bakst M.R., Baxter-Jones C., Bitgood J.J., Bradley F., Cheng K.M., Dietert R.R., Dodgson J.B., Donoghue A., Emsley A.E., Etches R., Frahm R.R., Gerrits R.J., Goetinck P.F., Grunder A.A., Harry D.E.,. Lamont S.J, Martin G.R., McGuire P.E., Moberg G.P., Pierro L.J., Qualset C.O., Qureshi M., Schultz F., Wilson B.W., 1999. Avian Genetic Resources at Risk: An assessment and proposal for conservation of genetic stocks in the USA and Canada. Report No. 20, University of California Division of Agriculture and Natural Resources, Genetic Resources Conservation Program, Davis, CA.

Proctor, N.S., Lynch, P.J., 1993. Manual of Ornithology. Yale University Press, New Haven.

Punnett, R.C., 1923. Heredity in Poultry. Macmillan and Co, St. Martin's Street, London, UK, pp. 204.

Romanoff, A.L., 1972. Pathogenesis of the avian embryo. An analysis of causes of malformations and prenatal death. 476. John Wiley and Sons, New York.

Ruyter-Spira, C.P., de Groof, A.J., van der Poel, J.J., Herbergs, J., Masabanda, R., Groenen, M.A., The, H.M.G.I-C., 1998. gene is a likely candidate for the autosomal dwarf locus in the chicken. J. Hered. 89, 295–300.

Scanes, C.G., Brant, G., Ensminger, M.E. (Eds.), 2004. 4th ed., Poultry Science. 372. Pearson Prentice Hall, Upper Saddle River, p. pp.

Schneider, R.A., Hu, D., Helms, J.A., 1999. From head to toe: conservation of molecular signals regulating limb and craniofacial morphogenesis. Cell Tissue Res. 296, 103–109.

Somes, R.G. Jr., 1998. International registry of poultry genetic stocks. Storrs Agricultural Experiment Station. Bulletin 476, xxxUniversity of Connecticut, Storrs, CT.

Somes, R.G. Jr, 1990. In: Crawford, R.D., (Ed.), Lethal mutant traits in chickens. Poultry Breeding and Genetics. Elsevier Publishers, BV, Amsterdam, pp. 293–316.

Tanaka, M., Hayashida, Y., Wakita, M., Hoshino, S., Nakashima, K., 1995. Expression of aberrantly spliced growth hormone receptor mRNA in the sex-linked dwarf chicken. Gifu 20. Growth Regul. 5, 218–223.

Vasicek, D., Vasickova, K., Kaiser, P., Drozenova, R., Citek, J., Hala, K., 2001. Analysis of genetic regulation of chicken spontaneous autoimmune thryoiditis, an animal model of human Hasimoto's thryoiditis. Immunogenetics 53, 776–785.

Wang, X., Erf, G.F., 2004. Apoptosis in feathers of Smyth line chickens with autoimmune vitiligo. J. Autoimmun. 22, 21–30.

Yoshizawa, K., Inaba, K., Mannen, H., Kikuchi, T., Mizutani, M., Tsuji, S., 2003. Analyses of beta-1 syntrophin, syndecan 2 and gem GTPase as candidates for chicken muscular dystrophy. Exp. Anim. 52, 391–396.

Zhang, Y., Gilliam, A.C., 2002. Animal models for scleroderma: an update. Curr. Rheumatol. Rep. 4, 150–162.