Poultry

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5.1 Introduction

5.1.1 Brief History and Zoological Description

From the time of initial domestication of wild birds, poultry have served humans as a source of food and a subject of cultural use, similar to other livestock species. The role of poultry production in global food provision has been steadily growing since the nineteenth century. Different needs of humans have led to a rise in poultry breeding and use of pure (fancy) breeds, indigenous populations, laboratory lines, and commercial poultry. Being notable for high efficiency and rapid development dynamic, the poultry industry now exceeds other livestock sectors in production growth rate and efficacy. Intensification of commercial poultry production has placed emphasis on selection and improvement of breeds and strains and on the development of novel lines and crosses. This, in turn, has required new genetic and selection approaches and technologies, and utilization of genetic resources adapted to variable and diverse specific environments. The importance of a deeper knowledge of avian biology including heredity, variation, and genomics is paramount. Substantial progress in poultry production can be achieved through advances in several areas, including selection, veterinary, nutrition, avian genetics, and genomics.

Avian species share a common ancestor with humans. The split between synapsids (mammals and their extinct ancestors) and diapsids (reptiles) occurred around 350 million years ago (MYA). Birds are believed to arise from therapod dinosaurs about 150 MYA. The origin of the whole *Galliformes* order is placed in the late Cretaceous at about 90 MYA, while the junglefowl genus, *Gallus*, evolved among the land fowl about 8 MYA (van Tuinen and Dyke 2004). Man began domestication of chickens in Southeast Asia and adjacent areas 8,000–10,000 years ago (Fig. 1). Later, waterfowl species including geese and ducks were domesticated. The turkey and Muscovy duck were domesticated in the New World, and some other birds (e.g., guinea fowl, Japanese quail, and ostrich) were also subject to domestication. Today's poultry breeds and their wild progenitors are separated across globally established poultry meat and egg industries.

There have been four stages of poultry history that have affected genetic diversity, leading to the chickens that exist today (Crawford 1990). The first stage was the process of domestication, involving selection for tameness, changes in body size, and accumulation of morphological and color variants. The second stage was diffusion outward from centers of domestication; genetic drift, migration, and isolation were major genetic forces leading to development of distinctive regional types. The third stage was the "hen craze era" late in the nineteenth century, when nearly all present-day breeds and varieties were created. The fourth stage is in place now, where multinational corporations breed and distribute egg and meat stocks that have remarkable productivity, but are derived from a narrow genetic base (Crawford 1995). During the fourth stage, anthropogenic factors have become more and more important in evolution and development of domestic fowl. Factors

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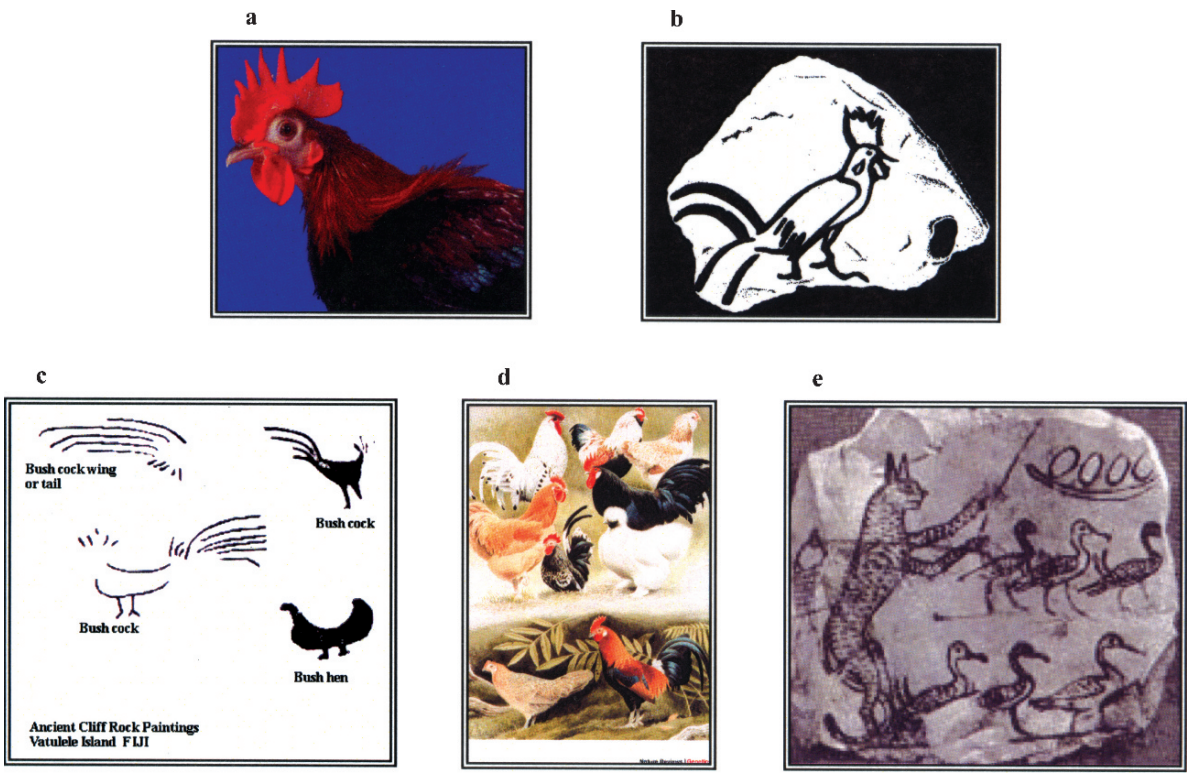

Fig. 1 Domestication of avian species. (**a**) A red junglefowl rooster (*Gallus gallus*), the wild chicken progenitor species (from Pisenti et al. 1999; http://www.grcp.ucdavis.edu/publications/doc20/front.pdf). (**b**) An egg-type cock painted on an ostracon from the tomb of Tutankhamen, Egypt, 1338 BC (Carter and Mace 1923–1933); published by Cassell Plc, currently a division of The Orion Publishing Group (London); attempts at tracing the copyright holder of the image were unsuccessful). (**c**) Ancient Pacific cliff rock paintings, Vatulele Island, Fiji (Ewins 1995; http://www.justpacific.com/fiji/fijianart/cliffart/cliffpaintings.pdf). (**d**) Red junglefowl (*shown at the bottom*) and several domestic chicken breeds (adapted with permission from Macmillan Publishers Ltd: Nature, Andersson 2001, © 2001). (**e**) A typical depiction of domesticated geese in ancient Egypt

such as civilization development, historical events, technological progress (Altukhov 2004), changes in climate, and extreme natural disasters greatly influence poultry genetic variability and may even lead to extinction.

Well-known poultry species include chickens, ducks, geese, turkeys, guinea fowl, quail and pigeons. They play an important role in the world's economy and provide a valuable protein source for people in both developing and developed countries. Birds are often raised as scavengers, i.e., at little cost, in areas where cattle cannot survive, such as those infested by the tsetse fly (*Glossina* spp.). Ostriches, emus, rheas, and cassowaries are all at various stages of domestication for their skins, meat, and other products (Scherf 2000).

Poultry and other avian species raised and kept by man belong to ten orders: *Galliformes, Anseriformes, Columbiformes, Passeriformes, Ciconiiformes, Pelecaniformes, Psittaciformes, Struthioniformes, Rheiformes,* and *Casuariiformes* (Table 1). Representatives of the most useful family of birds are in the *Phasianidae* family, a widely dispersed group of the order *Galliformes*. A more detailed zoological description and origin of the chicken will be narrated below. The turkey will be separately described in Chapter 6 of this volume. Details on other domesticated species of birds (Fig. 2) can be found elsewhere (Barloy 1978; Brothwell and Brothwell 1998; Brown 1929; Crawford 1990, 1995; Darwin 1868; del Hoyo et al. 1992–1996; Dembeck 1965; Hyams 1972; Mason 1984; Petrov 1962; Scherf 2000; Zeuner 1963).

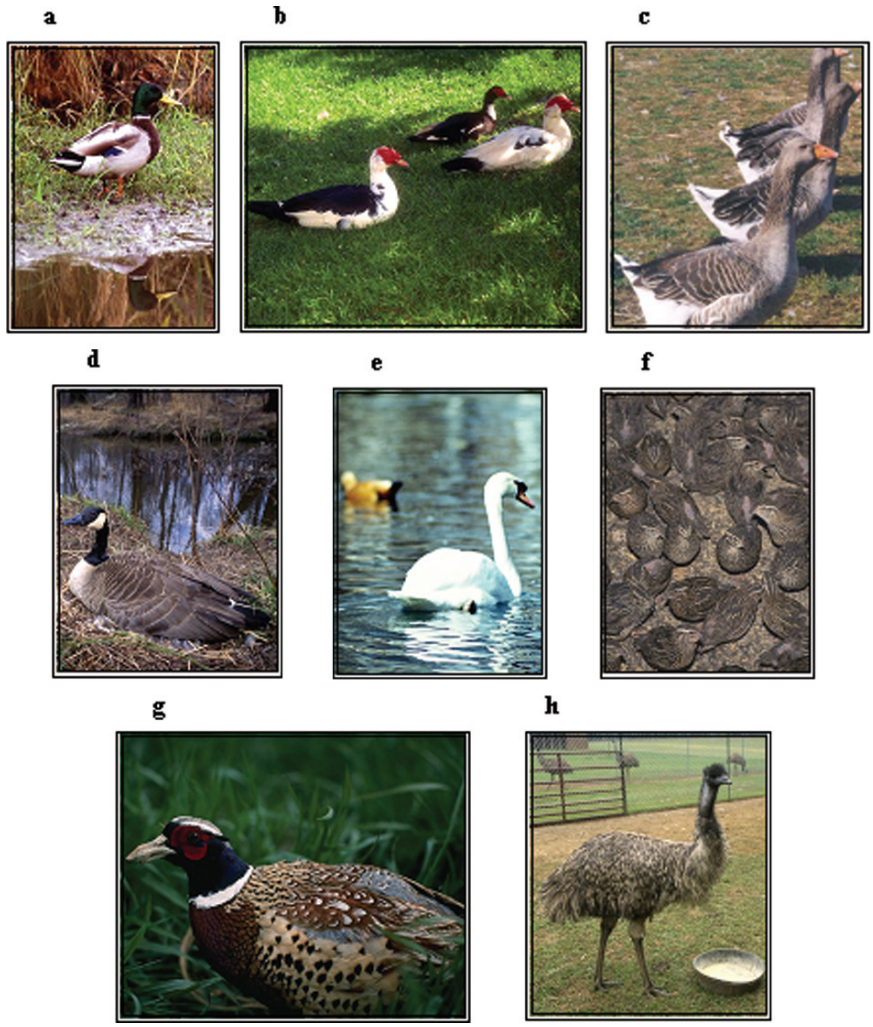

Fig. 2 Major domesticated avian species other than chicken and turkey. (**a**) A male of the mallard (*Anas platyrhynchos*), the progenitor of domestic ducks. (**b**) A domesticated American anseriform species of Muscovy ducks (*Cairina moschata*). (**c**) A flock of domestic Russian geese (photograph courtesy of Annette Güntherodt, Beberstedt, Germany; © 2004 From Encyclopedia of Animal Science by W.G. Pond and A.W. Bell (ed). Reproduced with permission of Routledge/Taylor & Francis Group, LLC). (**d**) A semidomesticated North American Canada goose (*Branta canadensis*). (**e**) Mute swan (*Cygnus olor*). (**f**) Japanese quail (*Coturnix japonica*). (**g**) Ring-necked pheasant (*Phasianus colchicus*). (**h**) Emu (*Dromaius novaehollandiae*). **a, b**, and **d-h**, USDA Image Gallery (http://www.ars.usda.gov/is/graphics/photos/) and Photography Center (http://www.usda.gov/oc/photo/opchomea.htm)

5.1.2 Chickens

Taxonomy and Wild Ancestors

The chicken is a member of the class *Aves*, subclass *Neornithes*, superorder *Neognathae*, order *Galliformes*, family *Phasianidae*, subfamily *Phasianinae*, genus *Gallus*. Closely related genera are *Meleagris* (turkey), *Pavo* (peafowl), and *Phasianus* (pheasant). Domestic chickens are descendants of junglefowl that now inhabit a wide crescent stretching from Pakistan to Indonesia including India, Indo-China, and South China, as well as the Philippines.

Four junglefowl species are known, including **red junglefowl** (*G. gallus*; Fig. 1a, d, and 3), **gray junglefowl** (*G. sonneratii*), **Ceylon junglefowl** (*G. lafayettei*),

Table 1 Taxonomy of major domesticated, semidomesticated, and caged avian species

Order	Family	Genus	Species	Distribution
Anseriformes	*Anatidae*	*Anser*	*A. anser* (graylag goose)[a]	Eurasia
„	„	„	*A. cygnoides* (swan goose)[a]	Asia
„	„	„	*A. fabalis* (bean goose)[b]	Eurasia
„	„	„	*A. albifrons* (white-fronted goose)[b]	Northern Hemisphere
„	„	„	*A. indicus* (bar-headed goose)[b]	Asia
„	„	„	*A. erythropus* (lesser white-fronted goose)[b]	Eurasia
„	„	*Branta*	*B. canadensis* (Canada goose)[c]	North America
„	„	*Cygnus*	*C. olor* (mute swan)[c]	Eurasia
„	„	*Alopochen*	*A. aegyptiacus* (Egyptian goose)[c]	Africa
„	„	*Cairina*	*C. moschata* (Muscovy duck)[a]	Tropical America
„	„	*Anas*	*A. platyrhynchos* (mallard)[a]	Northern Hemisphere
Galliformes	*Phasianidae*	*Meleagris*	*M. gallopavo* (turkey)[a]	North America
„	„	*Gallus*	*G. gallus* (red junglefowl)[a]	Southeast Asia
„	„	„	*G. sonneratii* (gray junglefowl)	Southwest India
„	„	„	*G. lafayettei* (Ceylon junglefowl)	Ceylon
„	„	„	*G. varius* (green junglefowl)	Java
„	„	*Pavo*	*P. cristatus* (Indian peafowl)[a]	India
„	„	*Phasianus*	*P. colchicus* (ring-necked pheasant)[c]	Eurasia
„	„	„	*P. versicolor* (green pheasant)[c]	Japan
„	„	*Lophura*	*L. nycthemera* (silver pheasant)	Southeast Asia
„	„	*Chrysolophus*	*Ch. pictus* (golden pheasant)	China
„	„	*Perdix*	*P. perdix* (gray partridge)[c]	Eurasia
„	„	*Coturnix*	*C. coturnix* (common quail)[c]	Eurasia, Africa
„	*Phasianidae*	„	*C. japonica* (Japanese quail)[a]	Asia
„	*Numididae*	*Numida*	*N. meleagris* (helmeted guinea fowl)[a]	Africa
„	*Odontophoridae*	*Colinus*	*C. virginianus* (northern bobwhite)[c]	North America
Passeriformes	*Fringillidae*	*Serinus*	*S. canaria* (island canary)[a]	Madeira, Azores, Canary Islands
„	*Estrildidae*	*Taeniopygia*	*T. guttata* (zebra finch)	Australia
Columbiformes	*Columbidae*	*Columba*	*C. livia* (rock pigeon)[a]	Eurasia, Africa
„	„	*Streptopelia*	*S. roseogrisea* (S. *risoria*) (African collared dove)[a]	Africa, North America
Pelecaniformes	*Phalacrocoracidae*	*Phalacrocorax*	*P. carbo* (great cormorant)[c]	Asia
Ciconiiformes	*Ardeidae*	*Egretta*	*E. garzetta* (little egret)[c]	Eurasia, Africa, Australia
Psittaciformes	*Psittacidae*	*Psittacula*	*P. krameri* (rose-ringed parakeet)	Africa, Asia
„	„	*Melopsittacus*	*M. undulates* (budgerigar)[c]	Australia
Struthioniformes	*Struthionidae*	*Struthio*	*S. camelus* (ostrich)[a]	Africa
Rheiformes	*Rheidae*	*Rhea*	*R. americana* (greater rhea)[c]	South America
„	„	*Pterocnemia*	*P. pennata* (lesser rhea)[c]	South America
Casuariiformes	*Dromaiidae*	*Dromaius*	*D. novaehollandiae* (emu)[c]	Australia
„	*Casuariidae*	*Casuarius*	*C.* spp. (cassowary)[c]	New Guinea, Australia

[a] Domesticated species

[b] Suggested contribution to polyphyletic origin of a domesticated form

[c] Semidomesticated species

and **green junglefowl** (*G. varius*). The red junglefowl, in turn, is subdivided into five subspecies depending on geographic distribution, variation in size of facial wattles and combs, and length and color of the neck hackles in males: Cochin-Chinese (*G. g. gallus*), Burmese (*G. g. spadiceus*), Tonkinese (*G. g. jabouillei*), Indian (*G. g. murghi*), and Javan (*G. g. bankiva*).

The natural habitat of red jungle fowl varies, including most types of forests present in Southeast Asia and in other territories of Asia, field edges, groves, and scrubland. The junglefowl is a highly adaptable species and can thrive in many habitats from sea level to 2,000 meters above sea level. Most junglefowl are found in damp forests, secondary growth, dry scrub, bamboo groves, and small woods. Although not rare, the species is under some hunting pressure (Scherf 2000).

Origin of Domestic Fowl — Monophyletic, Polyphyletic or Intermediate?

Because of varying opinions of zoologists, naturalists, geneticists, and other specialists, there is great interest in exploring the biology of junglefowl species and the origin of the domestic fowl (Moiseyeva et al. 2003). Beginning with Charles Darwin's fundamental work on this subject published in *The Variation of Animals and Plants Under Domestication* (1868), many investigations have been devoted to the specific features of junglefowl. The widely spread species *G. gallus* has been most fully described for discrete morphological and metric quantitative traits (Darwin 1868; Beebe 1918–1922; Delacour 1977; Nishida et al. 1983, 1985a, b; Moiseyeva and Volokhovich 1987; Moiseyeva et al. 1994) and, over last four decades, for biochemical (Baker 1964, 1968; Baker and Manwell 1972; Moiseyeva et al. 1994) and molecular (Siegel et al. 1992; Akishinonomiya et al. 1994, 1996; Romanov and Weigend 2001b; Hillel et al. 2003) markers.

Comparisons of four species of genus *Gallus* and chicken breeds indicate that *G. gallus* (red junglefowl) is the closest to chickens for most traits. This may be evidence of the monophyletic origin of chickens (Darwin 1868; Tegetmeier 1873; Beebe 1918–1922; Ivanov 1924; West and Zhou 1989). Another group of scholars (Dixon 1848; Abozin 1885; Brown 1906; Finsterbusch 1929; Hutt 1949; Smith and Daniel 1975; Plant 1984, 1986) adheres to the theory of polyphyletic origin referring to the fact that some characters known in chickens are absent in *G. gallus*, but present in other

Fig. 3 A lateral view of red junglefowl cock (*G. g. gallus*). An exhibit of the State Darwin Museum, Moscow, Russia. Photograph courtesy of A.A. Nikiforov (Altukhov 2004)

wild species or in extinct progenitor(s). Several investigators support an intermittent point of view, that is, between strong monophyletists and strong polyphyletists, considering *G. gallus* the major ancestor but not excluding small participation of other species in chicken domestication (Baker et al. 1971; Kogan 1979; Crawford 1990; Stevens 1991; Altukhov 2004).

Noteworthy, most genetic studies have relied upon *G. gallus* specimens bred by fancy breeders or in zoos, which may be contaminated with domestic chicken genes. Wild populations in their natural habitats are also quite often mated with village chickens and produce offspring that differ from the pure *G. gallus* (Beebe 1918–1922; Brisbin 1997). This situation leads to an overestimate of kinship between *G. gallus* and chicken breeds as compared with the three other wild species that do not always produce fertile hybrids with domestic chickens.

Based on the comparison of mitochondrial DNA (mtDNA) D-loop sequences, Akishinonomiya et al. (1994,1996) stated that only one subspecies, *G. g. gallus*, contains all the biodiversity of chickens. Niu et al. (2002) sequenced the first 539 bases of the mtDNA D-loop region in six Chinese local chicken breeds and compared that data to sequences of four juglefowl species in GenBank. The four species of the genus *Gallus* significantly differed from each other, and the Chinese native chickens were closest to the red junglefowl in Thailand and its adjacent regions, suggesting that the Chinese domestic fowl probably originated from the red junglefowl in these regions. It was suggested that the two subspecies of Thailand, *G. g. gallus* and *G. g. spadiceus*, form one subspecies because of their similarity to each other. However, these findings did not provide absolute proof because not all five *G. gallus* subspecies were surveyed and only one or two representatives per taxon were compared. Unfortunately, there was no mention in those studies of the correspondence of the sampled birds to the standards of a species or breeds. In addition, the authors did not acknowledge that local residents often mate different *Gallus* species with domestic chickens. Phylogenetic relationships of species in the genus *Gallus* could not be validated in this study due to insufficient statistical analyses (Nishibori et al. 2005).

On the other hand, supporters of the polyphyletic origin of chickens have not presented any archeological evidence about extinct ancestor(s), at least for heavy Asiatic meat-type breeds. Lack of many traits in *G. gallus* currently in chickens is not a conclusive argument for the polyphyletic origin. Domestic animal species often have significant breed diversity compared to their ancestral forms. One of the strong arguments in favor of the polyphyletic origin is the observation of fertile progeny produced from a wild fowl species other than *G. gallus* and domestic chickens or red junglefowl (Darwin 1868; Mason 1984; Johnsgard 1999), although hybrid stocks usually terminate in the second and backcross (BC) generations (Crawford 1995).

Remarkably, Darwin (1868) did express an opinion that "we have not such good evidence with fowls as with pigeons, of all the breeds having descended from a single primitive stock." In recent studies, Nishibori et al. (2005) provided evidence at the molecular level for hybridization of species in the genus *Gallus* except *G. varius*. They determined sequences of the whole mtDNA and two genomic sequences (intron) of ornithine carbamoyltransferase and four chicken repeat one elements for the species in the genus *Gallus*. According to the mtDNA sequence-based phylogenetic analyses, two gray junglefowls formed a cluster with red junglefowls and chicken, whereas one gray junglefowl was located in a remote position close to Ceylon junglefowl. The analyses based on the nuclear sequences resulted in alternative clustering of gray junglefowl alleles with those of Ceylon junglefowl and with those of red junglefowls and chicken. Red junglefowl and chicken alleles were also alternatively clustered. These findings could strongly suggest interspecies hybridizations between gray junglefowl and red junglefowl/chicken and between gray junglefowl and Ceylon junglefowl. A question was raised whether these three *Gallus* species are actually subspecies, but examination of more individuals of each species is needed to validate this hypothesis.

Another important quesion is what chicken breeds, i.e., evolutionary branch(es) of chickens, are most closely related to *G. gallus* and, therefore, which domesticated fowl are the most ancient. Studies to address these issues may be complicated because of possible contamination of the wild populations with domestic genes, usage of different markers, different sets of breeds across studies, genetic variation within chicken breeds, crossbreeding used for breed development, and different statistical methods for data analyses. A systems approach for addressing

this problem has been proposed (Moiseyeva 1998, 2003).

Time of Origin and Evolutionary Lineages

Darwin (1868) was uncertain about the exact center(s) of chicken origin, saying that "all our breeds are probably the descendants of the Malayan or Indian variety" of the red junglefowl. After Darwin, various authors named different geographical regions as the center of origin, including Burma (Peters 1913), India (Ivanov 1924; Wood-Gush 1959; Zeuner 1963), China (Ho 1977), Southeast Asia (West and Zhou 1989), and Thailand (Akishinonomiya et al. 1994, 1996). The origin of domestic chickens is dated approximately 6000–8000 BC (Ho 1977; Plant 1986; West and Zhou 1989; Crawford 1995). Scherf (2000) proposes that "the first domestication occurred in Southeast Asia some time prior to 6000 BC, before introduction of chickens into China." This was followed by the spread of chickens in the ancient times to the west, north and east including the Mediterranean and, more recently, the Pacific islands (Fig. 1b, c). Around 2500–2100 BC, chickens might have been separately domesticated in the Indus Valley (Pakistan) or diffused over there from Southeast Asia (Scherf 2000). The first domesticated chickens were probably assigned cultural or religious significance or were used for cockfighting, although the possibility of gathering eggs from wild and domestic chickens at the early stage of domestication is possible (Petrov 1941). In ancient beliefs, the rooster symbolized a clock, sun, fire, courage, or fecundity; the hen was related to maternity, housekeeper, and economy; and the egg was associated with development of life. Cockerels and hens were also used in predictions and divinations.

Chickens spread rapidly and their meat and eggs became highly appreciated as an important source of animal protein (Scherf 2000). As early as the times of Plato and Aristotle, chicken varieties were discernible (Moiseyeva and Lisichkina 1996; Scherf 2000). There is strong cumulative evidence that chickens were already present in the Americas at the time of Spanish discovery, and they came from across the Pacific (Carter 1971). However, acceptance of this point of view awaits the discovery of bones from securely dated pre-Columbian sites (Crawford 1995).

Despite the fact that chickens have been subject to domestication for less than 10,000 years, the amount of phenotypic variation accumulated over time is surprising (Jensen 2005). To date, four major evolutionary lineages can be observed among various chicken breeds selected by man (Moiseyeva et al. 2003; Fig. 4): egg-type, or Mediterranean, game, meat-type, and Bantam. Early domesticated chickens were small and shared morphological characteristics with modern egg-type fowl of Mediterranean roots and/or with true Bantams. This hypothesis, developed by Moiseyeva et al. (2003), is in agreement with ancient depictions of domestic chickens, which had the egg-layer morphological type (Brown 1929; Fig. 1b). The game chicken breeds might descend directly from the red junglefowl or from egg-type domestic birds. The meat-type breeds represent the latest chicken lineage and were probably selected from game breeds.

Based on analyses of biological, historical, archeological, etymological, ethnological, and ethnographical evidences, the domestication process of wild forms into chickens might have occurred independently in

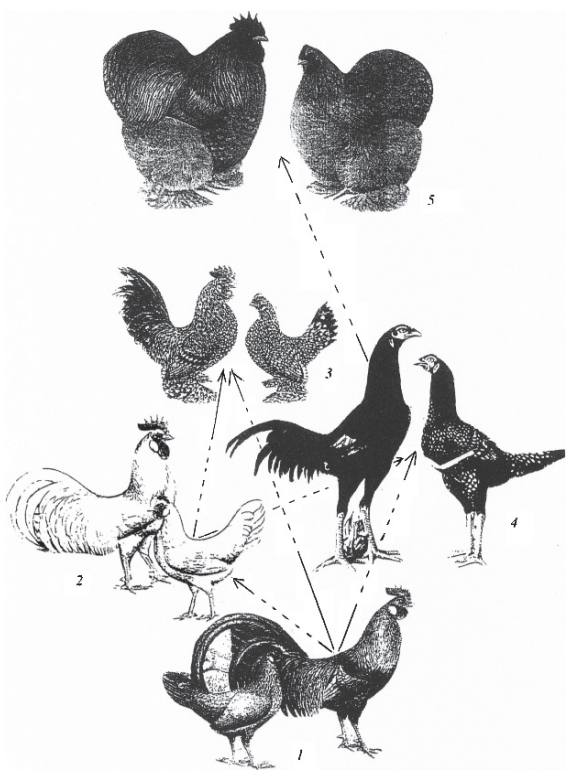

Fig. 4 Morphotypological forms of the domestic fowl and possible major evolutionary lineages from the main wild ancestor, *Gallus gallus* (1), to egg-type (2), Bantam-type (3), game (4), and meat-type (5) breeds (Altukhov 2004)

several parts of Asian region and at different times (West and Zhou 1989; Crawford 1995; Moiseyeva 1998; Moiseyeva et al. 2003). Each evolutionary lineage of chickens could contain a different polyphyletic origin, and some types, e.g., Mediterranean and Bantam breeds, might come directly from *G. gallus*. The hypothesis of multiple origins in South and Southeast Asia is supported by molecular analyses of the mtDNA hypervariable segment I for 834 Eurasian domestic chickens, as well as 66 wild red junglefowls from Southeast Asia and China (Liu et al. 2006).

5.1.3 Economic Importance and Nutritional Value

Meat, milk, and eggs produced by domestic animals have long represented important parts of the diets of many people (Pond and Bell 2004). The world poultry industry is a growing part of global agribusiness and also one of the most dynamic components of world agribusiness trade. Over the last four decades, an estimated live poultry population of the world (Table 2) has increased by 330% (chickens), 440% (ducks), 112% (turkeys), and 724% (geese). On the other hand, the number of fancy breeds and indigenous populations has significantly decreased during the twentieth century.

Poultry meat is defined as meat from chicken, turkey, duck, goose, guinea fowl, and pigeon. Poultry is one of the most consumed meats in the world and is the most consumed meat per capita in the United States (Pond and Bell 2004). The production and consumption of poultry meat, specifically chicken, turkey, duck, and goose, has dramatically increased over the last several decades, with total production of estimated 81.4 million metric tons (MT) in 2005 (Table 3). The bulk of poultry meat is produced from chickens, mostly broilers that are raised for meat production and have been selected for increased meat yield. In the 1950s, it took approximately 11 weeks to raise a 1.6-kilogram (kg) broiler. Currently, a 2.3-kg broiler can be raised in 6–7 weeks depending on feed quality, genetic background of crosses, and local management conditions. Broilers are shipped to the market at various ages and

Table 2 World poultry production: live animal stocks[a]

Stocks (1000)	Year						
	1961	1970	1980	1990	1995	2000	2005
Chickens	3,883,540	5,207,622	7,216,976	10,673,952	12,959,165	14,476,988	16,695,877
Ducks	193,453	256,318	351,979	552,612	797,412	927,973	1,044,736
Geese	36,640	54,578	69,273	131,557	235,103	234,497	301,905
Turkeys	130,745	99,832	200,644	243,042	247,387	268,015	276,821

[a] FAOSTAT (2006)

Table 3 World poultry production: meat[a]

Poultry meat production (MT)	Year						
	1961	1970	1980	1990	1995	2000	2005
Poultry all	8,953,120	15,100,097	25,962,116	41,025,900	54,730,103	69,176,770	81,436,269
Chicken	7,557,158	13,141,695	22,907,219	35,459,934	46,572,934	59,029,981	70,474,502
Turkey	902,220	1,224,183	2,054,235	3,703,989	4,568,167	5,125,341	5,167,560
Duck	335,922	500,841	713,113	1,231,933	2,096,213	3,000,542	3,447,564
Goose	149,717	226,270	282,322	616,534	1,476,930	2,001,974	2,326,683
Pigeon and other birds	8,102	7,108	5,228	13,680	15,859	18,932	19,958

[a] FAOSTAT (2006)

weights and as a variety of products, including whole carcasses weighing around 1 to 4–5 kg broilers subject to meat deboning (Pond and Bell 2004). Modern domestic turkeys have been selected primarily for large body size and rapid growth rate. Commercially, they are usually grown until they reach sexual maturity. For males, this is approximately 20 weeks of age, when they can weigh over 20 kg, compared to a 3-year-old male wild turkey that weighs a mere 9 kg (Pond and Bell 2004).

Eggs produced globally are predominantly from chickens (Table 4), with an increase in egg production of about 50% in the 1990s. While duck eggs lag far behind chicken eggs in importance, they are in high demand in China, several Pacific Rim countries, and Europe. There is commercial production of quail eggs in many countries, although on a smaller scale. In the past, ostrich, pelican, peafowl, swan, and guinea fowl eggs were also valued (Bell and Weaver 2002).

Chicken is the most developed global poultry industry sector, while ducks, geese, and turkeys are raised more regionally (Table 5). The world leader in poultry stocks, except turkeys, is China. Turkeys are mainly produced in the USA, Europe, and Latin America. Turkey is second after the chicken in economic importance among poultry species in the USA.

Capital investment necessary for an increase in production is roughly US $1 per kilogram for both eggs and broilers. Investment for new facilities in the poultry industry has been US $4 billion annually worldwide. During the 1990s, over US $40 billion was invested in the world chicken industry. It is likely that the world increase in chicken meat and egg production will continue into the twenty-first century, but not at such a rapid pace (Bell and Weaver 2002).

In addition to low production costs, one of the main reasons that poultry meat consumption has increased in the last decade is the nutritional value of the meat (Table 6). The fat in poultry meat is located in the skin and is therefore easily removable compared to other meats, enabling consumers to adopt a more low-fat type of meat in their diets. In addition, the fat in poultry meat is lower in saturated fatty acids and higher in unsaturated fatty acids. This fat deposition can vary among species and is diet-dependent. Therefore, poultry meat can easily be incorporated

Table 4 World poultry production: eggs[a]

Eggs primary production (MT)	Year						
	1961	1970	1980	1990	1995	2000	2005
Chicken eggs	14,408,065	19,538,393	26,215,604	35,243,467	42,854,069	51,678,162	59,433,971
Total	15,133,710	20,412,719	27,414,941	37,524,123	46,891,269	55,797,691	64,576,599

[a] FAOSTAT (2006)

Table 5 World poultry production: live animal stocks (1000) by country in 2005[a]

Country	Chickens	Country	Ducks	Country	Geese	Country	Turkeys
China	4,360,243	China	725,018	China	267,819	USA	88,000
USA	1,950,000	Viet Nam	50,000	Egypt	9,100	France	30,820
Indonesia	1,249,426	Indonesia	34,275	Romania	4,000	Chile	26,500
Brazil	1,100,000	India	33,000	Poland	3,000	Italy	26,000
India	430,000	France	22,406	Madagascar	3,000	Brazil	16,200
Mexico	425,000	Ukraine	22,000	Taiwan	2,819	Germany	10,611
Russia	328,933	Thailand	17,000	Russia	2,750	UK	8,300
Turkey	296,876	Malaysia	16,000	Hungary	2,127	Portugal	7,000
Japan	283,000	Bangladesh	11,700	Israel	1,400	Slovakia	5,800
Iran	280,000	Philippines	10,439	Turkey	1,400	Canada	5,600

[a] Top ten countries in raising each of major poultry species ; FAOSTAT (2006)

into a well-balanced diet to improve health (Pond and Bell 2004).

Eggs are not only palatable, but are also considered to be a healthy food (Bell and Weaver 2002). Its protein value is the highest of all food, it is easy to digest, and its calories and fat content are moderate (Table 7). This image has been tarnished somewhat in the last 20 years due to increased awareness of cholesterol, food safety, and lack of convenience in preparation (Bell and Weaver 2002).

Waterfowl production is traditionally popular in Asia and some countries of Europe and Near East. One of the major features of geese is their capability to forage on grass alone, which is impossible for chickens. Also, geese are willing to eat more than is required. Owing to this peculiarity, they have been used for fattening since very early times and have become too heavy to fly (Scherf 2000). Duck production is not a dominant global sector, especially in most developed countries (Kear 1975), most likely because of a monogamous mating system, the deposition of large amounts of fat below the swim line, a large bone:meat ratio in the carcass, a long incubation period of 28 days, and a breeding season confined to the spring (Scherf 2000). Muscovy duck farming is nowadays very popular in all equatorial countries of Africa and Asia. In Europe and Taiwan, a sterile hybrid, the mulard, is commercially produced by crossing the Muscovy with the common domestic duck (Crawford 1992; Scherf 2000).

Next among poultry farming is the ostrich. The annual world demand for ostrich skins is almost one million, while their world production, largely from South African farms, is less than 250,000 skins a year (Scherf 2000). Small numbers of skins are also supplied to the market from Zimbabwe, Tanzania, and Texas. In Australia, there were more than 35,000 farmed ostriches in 1995 and numbers rapidly increased to 200,000 birds in 2000. In 1995, the local price for ostrich meat in Australia was Aus $40 per kilogram (US$29) and a pair of breeding ostriches sold for Aus$60,000–120,000. Currently, the demand

Table 6 Proximate composition and energy values of raw poultry meat in avian species[a]

Species	Meat type/skin	Moisture %	Protein %	Fat %	Ash %	Energy (kcal/100 g)
Chicken	Light, with skin	68.6	20.3	11.1	0.86	186
Chicken	Light, without skin	74.9	23.2	1.6	0.98	114
Chicken	Dark, with skin	65.4	16.7	18.3	0.76	237
Chicken	Dark, without skin	76.0	20.1	4.3	0.94	125
Turkey	Light, with skin	69.8	21.6	7.4	0.90	159
Turkey	Light, without skin	73.8	23.6	1.6	1.00	115
Turkey	Dark, with skin	71.1	18.9	8.8	0.86	160
Turkey	Dark, without skin	74.5	20.1	4.4	0.93	125
Duck	All, with skin	48.5	11.5	39.3	0.68	404
Duck	All, without skin	73.8	18.3	6.0	1.06	132
Goose	All, with skin	49.7	15.9	33.6	0.87	371
Goose	All, without skin	68.3	22.8	7.1	1.10	161

[a] Pond and Bell (2004)

Table 7 Percentage composition of the chicken egg[a, b]

Component	Water	Protein	Lipid	Carbohydrate	Ash	Calories (kcal/egg)
Albumen	88.0	9.7–10.6	0.03	0.4–0.9	0.5–0.6	19
Yolk	48.2	15.7–16.6	31.8–35.5	0.2–1.0	1.1	65
Whole egg	75.5	12.8–13.4	10.5–11.8	0.3–1.0	0.8–1.0	84

[a] 60 g egg. Shell is not included. Percentages of different components vary in different breeds

[b] After Bell and Weaver (2002)

for ostrich meat is far in excess of supply; world production is only 12,000–15,000 MT as the industry has not yet made a full transition from a breeder market to commercial production. Around 60% of this production is in South Africa (World Ostrich Association, http://www.world-ostrich.org/demand.htm). However, the skin is the most valuable ostrich product (Scherf 2000). High-quality, unprocessed ostrich skins harvested at 14 months of age are worth about US $200 wholesale. The price for a domestic ostrich in South Africa was worth R 150 in 1979 and included 48% for the skin, 40% for the feathers, and 12% for the carcass. In 1994 in Texas, the estimated value of an ostrich was US $900. Processing of ostrich skins is done in South Africa and Germany, while ladies handbags, shoes, briefcases, and wallets are produced from the skins in France and Italy. The greatest demand for these articles is from Japan (Scherf 2000).

The emu farming industry produces meat, skins, and byproducts (oil and feathers) which are sold in Australia and overseas, the key importers being the USA, Japan, France, and Southeast Asia (Scherf 2000). For some farms, tourism is also a source of income. Since 1991, farmed emus have been slaughtered in Australia, and there was an estimate of 85,000 birds available for slaughter in 1995. Emu meat is characterized by a lower fat and cholesterol content, and by a gamey flavor. Emu oil is produced by rendering fat; it is utilized in cosmetics and for muscle and joint pain treatment. An emu was valued as US$450 in Texas in 1994, where there were about 30,000 birds. The outlook for emu farming is very promising, although production and processing costs will need to be decreased (Scherf 2000).

5.1.4 Breeding Objectives

Over the 20th century, modern selective breeding has resulted in spectacular progress in both egg and meat production traits (Burt 2002). By 2002, world egg production was 795 billion/year and broiler meat was at 6.5 million MT/year (Burt 2005). However, these successes have led to an increase in the incidence of undesirable conditions including congenital disorders (e.g., ascites, lameness), reduced fertility, and reduced resistance to infectious disease in meat-type chickens, and osteoporosis in laying hens. Since genetic progress in egg and meat production could approach its limit within the next 20 years (Burt 2002), the poultry industry priorities would be to reduce losses from undesirable traits, develop new products with higher quality (e.g., increased egg shell strength), and secure greater uniformity and predictability in production. Another growing concern is food safety that requires a reduction in the use of chemicals and antibiotics and to increase genetic resistance to pathogens (Burt 2005).

At present, three major categories of poultry stocks coexist: pure fancy or exhibition breeds, indigenous populations, and commercial poultry. Each of these categories is characterized by specific features that depend on the needs of man. Pure breeds maintained by fanciers may be classified by purpose of use, geographical origin, evolutionary roots, and other criteria. Indigenous flocks are kept locally in primitive conditions and without any selection. Commercial poultry stocks involve in selected egg and meat-type lines and crosses. These three types of poultry stocks also differ in their utility importance. Fancy fowl and indigenous populations represent genetic resources in poultry, i.e., they may be used as the sources of genetic variability for commercial poultry and in creating new breeds and lines. Poultry breeders maintain breed characteristics and economically important traits at the standard level. Commercial poultry is related to commodity output. The main selection task in developing this type of poultry is to increase the productivity and viability of industrial lines and crosses. At the same time, essential efforts are undertaken to lower costs of produce. New genetic and selection approaches and technologies, and genetic resources adapted to various environment conditions are sought by the commercial poultry industry.

Modern poultry breeding industry comprises a limited number of major companies worldwide. These companies maintain the foundation and great grandparent stock to produce commercial meat and egg-type lines (Bell and Weaver 2002). At first pure breeding was used, then, crossbreeding to exploit heterosis was employed between 1930 and 1950, and now crosses of strains and synthetic lines are done routinely but only a few breeds and varieties are used. White Leghorns (WL) dominate white egg production, Rhode Island Red (RIR) and a few others are

used for brown eggs, and White Cornish and White Plymouth Rocks for meat (Crawford 1995). However, there is a tendency to utilize more breeds in commercial poultry, especially those breeds adapted to local environments or suitable to meet consumer preferences (Altukhov 2004).

The genetic performance of the birds is a main target of breeding in the poultry industry. Traits for selection, or at least monitoring, by egg-type chicken breeders include age of sexual maturity, rate of lay before and after molt, livability in the growing and laying house, egg weight, body weight (BW), feed conversion, shell color, shell strength, albumen height, egg inclusions (blood and meat spots) and temperament, as well as traits associated with the productivity of the parent (Keeton et al. 2003). Since the early 1980s, the increasing proportion of eggs used in food processing has added such traits as percentage solids and lipids in the egg. Egg production per hen housed remains the single selected trait, although its major component is now considered to be persistency of lay rather than peak rate of lay. Importance of selection for disease resistance varies from one breeding company to another. In meat-type chickens, breeding objectives include broiler growth rate, meat yield traits, livability, hatching egg production, and fertility (Keeton et al. 2003), as well as decreased abdominal and carcass fat, and lower feed conversion. Skeletal problems, such as leg weakness, in commercial broiler, egg laying, and breeder flocks represent another major challenge for poultry breeding and selection (Bennett and Ijpelaar 2003).

5.2 Classic Genetics

5.2.1 Brief History of Poultry Genetics

Analysis of inheritance in the chicken began more than one century ago and led to the development of the classical genetic map (Fig. 5). The first genes assigned to a single chromosome were sex-linked (reviewed by Crawford 1990; Romanov et al. 2004). In about the mid-twentieth century, poultry immunogenetics began. Cytogenetics as a branch of poultry genetics appeared in the early 1960s and became another research avenue in the field of avian heredity. The chicken has been a model for cytogenetic research given that its chromosomal morphology and behavior parallels that of other animal species (Crawford 1990). Chromosome numbers for some avian species are given in Table 8.

Recent progress in molecular biology, cytogenetics, and DNA technologies have resulted in novel tools to address chicken gene mapping and genomics issues. In the 1990s, configurations of chicken molecular and cytogenetic maps were significantly advanced. The application of bacterial artificial chromosome (BAC) libraries, BAC-contig physical maps, expressed sequence tags (EST), and whole-genome sequencing has provided new prospects in chicken genomics (reviewed by Romanov et al. 2004).

The chicken haploid genome has about 1.2×10^9 base pairs of DNA (Stevens 1986; Bloom et al. 1993; Bennett et al. 2003) arranged on 38 pairs of autosomes as well as the Z and W sex chromosomes (Yamashina 1944). Many of the autosomes are small microchromosomes and, unlike the larger macrochromosomes, cannot be identified by size (Ohno 1961; Crawford 1990). This intricacy of the genome composition has impeded mapping of chicken genes and sorting of chicken chromosomes. Current molecular and physical maps for the chicken encompass more than 2,000 genes and markers and other advanced chicken genomic resources also exist (Romanov et al. 2004).

5.2.2 Early Classical Mapping Efforts

After the rediscovery of Mendel's laws, Bateson and Saunders (1902) wrote one of the first articles devoted to hereditary characters or "allelomorphs" (now known as "alleles") in the chicken and some other organisms. This was the first introduction of the domestic fowl as a classical genetic model (see reviews by Pisenti et al. 1999; Romanov et al. 2004). The notion of "linkage" emerged thanks to Sutton (1903) who claimed that "all the allelomorphs represented by one chromosome must be inherited together." Lock (1906) also suggested that linkage might happen if genes lie on the same chromosome. Other geneticists extended these ideas in subsequent decades. Thomas Hunt Morgan demonstrated crossing over, a form of chromosomal recombination between closely linked genes (Morgan 1910, 1911). Morgan received the Nobel Prize in Physiology or

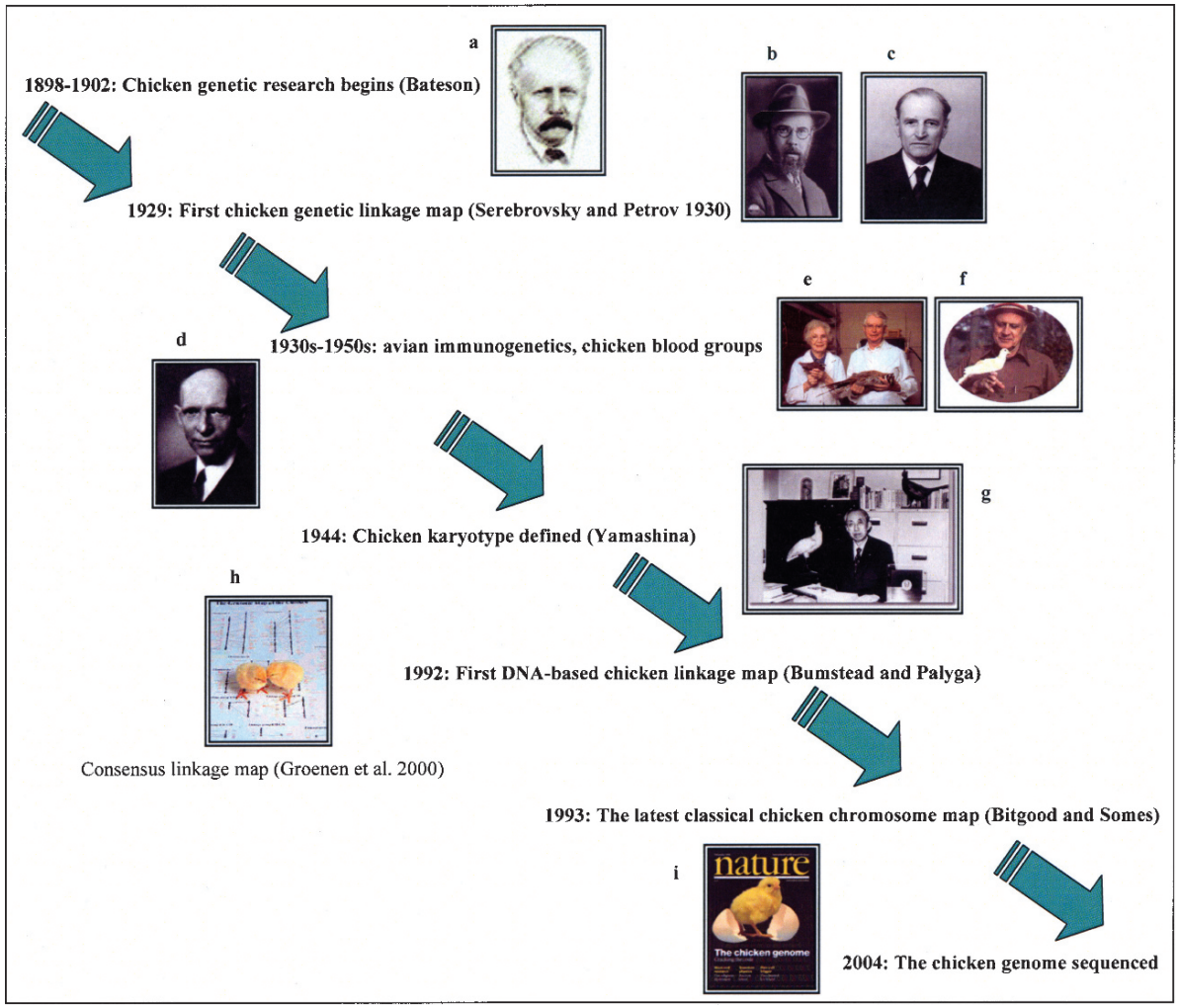

Fig. 5 Outline of poultry genetics history. Around the time of rediscovery of Mendel's laws of inheritance (1900), William Bateson (**a**), the father of modern genetics, conducted with his fellows a series of experiments in the chicken, thus introducing this domestic bird as a classical genetic model. By 1930, the first chicken genetic linkage map was generated by Serebrovsky (**b**) and Petrov (**c**). By the middle of the last century, avian immunogenetics was born and the chicken blood groups were discovered thanks to efforts of L. Cole (**d**), Irwin, McGibbon, E. Briles (**e**), C. Briles, Miller (**f**), and many others. In 1944, Yamashina (**g**) defined the chicken karyotype, as we know it today. With the advent of molecular genetic era, the first DNA-based chicken linkage map was created in UK in 1992. The follow-up development of molecular maps in the USA and the Netherlands led to the generation of the consensus linkage map in 2000 (**h**, USDA Image Gallery, http://www.ars.usda.gov/is/graphics/photos/). The classical chicken chromosome map was last updated in 1993. In 2004, the publication of the draft chicken sequence became a landmark in the history of poultry genetics (**i**, adapted with permission from Macmillan Publishers Ltd: Nature, © 2004)

Medicine in 1933 for postulating the role that chromosomes play in heredity.

The discovery of gene linkage and crossing over became the beginning of classical genetic map development. It was found that the stronger linkage between two genes, the shorter distance between them, and to measure this linkage, the frequency of crossing over was exploited. In honor of Morgan, the map distances were called "centi-Morgan," with 1% of linkage breakage being equal to one centimorgan (1 cM) (reviewed by Romanov et al. 2004).

Sex linkage, as the most obvious variant of genetic linkage, was first reported for the imperfect albinism in canaries by Durham and Marryat (1908)

Table 8 Genome size of the selected avian species

Species	Chromosome number (2*n*)	C value (pg)[a]	Reference
Gallus gallus (red junglefowl)	78	1.25	Crawford (1990), Gregory (2006)
Coturnix japonica (Japanese quail)	78	1.29–1.41	Crawford (1990), Gregory (2006)
C. coturnix (common quail)	78	1.35	Gregory (2006)
Meleagris gallopavo (turkey)	80	1.31–1.68	Crawford (1990), Gregory (2006)
Numida meleagris (helmeted guinea fowl)	78	1.23–1.31	Crawford (1990), Gregory (2006)
Pavo cristatus (Indian peafowl)	76	—	Sasaki et al. (1968)
Phasianus colchicus (ring-necked pheasant)	82	0.97–1.27	Crawford (1990), Gregory (2006)
Chrysolophus pictus (golden pheasant)	82	1.21	Gregory (2006)
Lophura nycthemera (silver pheasant)	80	—	Schmid et al. (2000)
Anas platyrhynchos (mallard)	80	1.24–1.54	Crawford (1990), Gregory (2006)
Cairina moschata (Muscovy duck)	80	1.00–1.34	Crawford (1990), Gregory (2006)
Anser anser (graylag goose)	80	1.08[b]	Crawford (1990), Gregory (2006)
A. cygnoides (swan goose)	80 or 82+	1.08[b]	Crawford (1990), Gregory (2006)
Cygnus olor (mute swan)	80	1.48	Gregory (2006)
Struthio camelus (ostrich)	80	2.16	Gregory (2006)
Rhea americana (greater rhea)	80	—	Gunski and Giannoni (1998)
Dromaius novaehollandiae (emu)	80	1.55–1.63	Gregory (2006)
Casuarius spp. (cassowary)	80	—	Takagi et al. (1972)
Apteryx australis (brown kiwi)	80	—	De Boer (1980)
Columba livia (rock pigeon)	80	1.14–1.65	Gregory (2006)
Streptopelia roseogrisea (African collared dove)	78	—	Schmid et al. (2000)
Serinus canaria (island canary)	80	1.48–1.62	Gregory (2006)
Taeniopygia guttata (zebra finch)	80	1.25	Pigozzi and Solari (1998), Gregory (2006)
Psittacula krameri (rose-ringed parakeet)	68	1.37	Gregory (2006)
Melopsittacus undulates (budgerigar)	58–60	1.02–1.37	Gregory (2006)
Grus grus (common crane)	80	1.54	Gregory (2006)
Ciconia ciconia (white stork)	68	1.58	Takagi and Sasaki (1974), Gregory (2006)
Leptoptilos crumeniferus (Marabou stork)	72	1.34	Gregory (2006)
Gymnogyps californianus (California condor)	80 or 82	1.51	Raudsepp et al. (2002), Gregory (2006)
Pelecanus onocrotalus (great white pelican)	66	1.25	Gregory (2006)
Falco peregrinus (peregrine falcon)	50	1.45	Gregory (2006)
Aquila chrysaetos (golden eagle)	62	1.48	Gregory (2006)

[a] 1 pg = 978 Mb

[b] C value for an unknown goose species (Gregory 2006)

[c] C value for the turtle dove (*Streptopelia turtur*; Gregory 2006)

and for the barring pattern (*BARR***) in Barred Plymouth Rock chickens by Spillman (1908) (reviewed by Romanov et al. 2004). Unlike mammals, the female bird is the heterogametic sex carrying the two different sex chromosomes (now referred to as Z and W), while the male is the homogametic sex (ZZ). There were subsequent assignments of other chicken genes to the sex (Z) chromosome and estimation of linkage between them (Punnett and Bateson 1908; Bateson 1909; Hagedoorn 1909; Bateson and Punnett 1911; Davenport 1911, 1912; Sturtevant 1911, 1912; Morgan and Goodale 1912; Goodale 1917; Haldane 1921; Serebrovsky 1922). Dunn and Jull (1927) found a close linkage between the genes for dominant white (*I*, or *SILV*) and crest (*CR*), and Serebrovsky and Petrov (1928) reported on creeper (*CP*) and rose comb (*R*) that were the first known instances of autosomal linkage. Loci mapped by classical mating are presented in Table 9.

Table 9 Classical chicken loci reviewed by Bitgood and Somes (1993)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
CP	*Cp*	Creeper	I	Presumably chromosomes 2, 3, or 4	N/A [presumably GGA4 if controlled by *FGFR3*]
R	—	Comb, rose	I	Presumably chromosomes 2, 3, or 4	N/A [presumably GGA4 due to linking to *CP*]
U	—	Uropygial	I	Presumably chromosomes 2, 3, or 4	N/A [presumably GGA4 due to linking to *R*]
LAV	*lav*	Lavender, plumage color	I	Presumably chromosomes 2, 3, or 4	N/A [presumably GGA4 due to linking to *R*]
MP	*Mp*	Ametapodia	I	Presumably chromosomes 2, 3, or 4	N/A [presumably GGA4 due to linking to *R*]
FR	*fr*	Fray	II	Presumably chromosomes 2, 3, or 4	N/A [possibly E22C19W28_ E50C23 due to linking to *SILV*]
CR	*Cr*	Crest, tassel feather length	II	Presumably chromosomes 2, 3, or 4	N/A [possibly E22C19W28_ E50C23 due to linking to *SILV*]
SILV	*I, PMEL17, MMP, MMP115*	Silver homolog (mouse) [dominant white plumage color; 115-kDa melanosomal matrix protein]	II	Presumably chromosomes 2, 3, or 4	E22C19W28_ E50C23
F	*f*	Frizzle, feather structure	II	Presumably chromosomes 2, 3, or 4	E22C19W28_ E50C23
BCDO2	*w, W, APOA1*	Beta-carotene dioxygenase 2	III	1	GGA24
CPHH	*Ea-H, EAH*	Erythrocyte alloantigen H (blood group system H)	III	1	N/A [possibly GGA24 due to linking to *APOA1*]
SE	*se*	Sleepy-eye	III	1	N/A [possibly GGA1 due to linking to *CPJJ*]
CPJJ	*Ea-J, EAJ*	Erythrocyte alloantigen J (blood group system J)	III	1	N/A [possibly GGA1 due to linking to *O*]

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
P	—	Pea comb	III	1	N/A [possibly GGA1 due to linking to *ALVE1*]
CHA	*cha*	Charcoal	III	1	N/A [possibly GGA1 due to linking to *P*]
DB	*Db, ma*	Dark brown Columbian-type plumage pattern (marbling)	III	1	N/A [possibly GGA11 due to linking to *MC1R*]
MC1R	*E*	Melanocortin 1 receptor (alpha melanocyte stimulating hormone receptor) [extended black plumage pattern]	III	1	GGA11
TAFF	*t*	Feathering, retarded-tardy feather growth	III	1	N/A [possibly GGA11 due to linking to *MC1R*]
ML	*Ml*	Melanotic, plumage pattern	III	1	N/A [possibly GGA11 due to linking to *MC1R*]
PG	*Pg*	Patterning gene, penciling, feather pattern	III	1	N/A [possibly GGA11 due to linking to *ML*]
CPPP	*Ea-P, EAP*	Erythrocyte alloantigen P (blood group system P)	III	1 (questionable assignment)	GGA3
NA	*Na*	Naked neck	III	1 (questionable assignment)	GGA3
H	*h*	Silkiness, feather structure	III	1 (questionable assignment)	N/A [possibly GGA3 due to linking to *NA*]
FL	*Fl*	Flightless	III	1 (questionable assignment)	N/A [possibly GGA3 due to linking to *H*]
CYP19A1	*Hf, HF, P450arom, MCW0357, CYP19*	Cytochrome P450, family 19, subfamily A, polypeptide 1 (aromatase; henny feathering, feather structure)	III	1	GGA10
GH1	*Gh, ROS0118, GH*	Growth hormone 1	III	1	GGA27

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
CPDD	*Ea-D, EAD*	Erythrocyte alloantigen D (blood group system D)	III	1	N/A
CPII	*Ea-I, EAI*	Erythrocyte alloantigen I (blood group system I)	III	1	GGA23
ALVE1	*ev1, ev-1,EV1*	Endogenous retrovirus 1	III	1	GGA1
PE	*pe*	Perosis	III	1	N/A [possibly GGA1 due to linking to *SE*]
MB	*Mb*	Muffs and beard, feather length	III	1	N/A [possibly GGA24 due to linking to *CPHH*]
CPCC	*Ea-C, EAC*	Erythrocyte alloantigen C (blood group system C)	III	1	N/A
CPEE	*Ea-E, EAE*	Erythrocyte alloantigen E (blood group system E)	III	1	GGA26
CPAA	*Ea-A, EAA*	Erythrocyte alloantigen A (blood group system A)	III	1	GGA26
PTI(?)[c]	*Pti-?*	Ptilopody, feathered shank	III	1	N/A [possibly GGA24 due to linking to *APOA1*]
ALVE4	*ev4, ev-4, EV4*	Endogenous retrovirus 4	III	1	GGA6
ALVE5	*ev5, ev-5, EV5*	Endogenous retrovirus 5	III	1	N/A [cytogenetically assigned to GGA1; could also be on GGA6 due to linking to *ALVE4*]
ALVE6	*ev6, ev-6, EV6, ALVE6A*	Endogenous retrovirus 6	III	1	GGA1
ALVE13	*ev13, ev-13, EV13*	Endogenous retrovirus 13	III	1	N/A [cytogenetically assigned to GGA1]
ALVE8	*ev8, ev-8, EV8*	Endogenous retrovirus 8	III	1	N/A [cytogenetically assigned to GGA1]
ALVE(?)	*ev(?)*	Avian leukosis virus (ALV) provirus	III	1	N/A

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
HBG2	*HGB, HBB, HBB@*	Hemoglobin, gamma G (hemoglobin, beta)	III?	1 or 2	GGA1
HBG1 or HBE1	*HBE or HBR*	Hemoglobin, gamma A or epsilon 1 (globin, epsilon or rho; embryonic beta-like globins)	III?	1 or 2	N/A [assigned to GGA1 or GGA2 by chromosomal fractionation; linked to HBD; assembled on GGA1]
D	—	Cup-, V-type duplex comb	IV	Presumably chromosomes 2, 3, or 4	N/A [probably GGA2 due to linking to *LMBR1* and M]
M	—	Spurs, multiple	IV	Presumably chromosomes 2, 3, or 4	N/A [probably GGA2 due to linking to *LMBR1*]
LMBR1	*Po, PO*	Limb region 1 homolog (mouse) [polydactyly, duplicate polydactyly]	IV	Presumably chromosomes 2, 3, or 4	GGA2
VLDLR	*Ro, RO*	Very low-density lipoprotein receptor (restricted ovulator)	V	Z	GGAZ
SH	*sh*	Shaker	V	Z	N/A
N	*n*	Naked	V	Z	N/A
PX	*px*	Paroxysm	V	Z	N/A
LN	*ln*	Lethal liver necrosis	V	Z	N/A
GHR	*dw, DW*	Growth hormone receptor (sex-linked dwarfism)	V	Z	GGAZ
WL	*wl*	Sex-linked wingless	V	Z	N/A
PN	*pl*	Prenatal lethal	V	Z	N/A
K	*ev21*	Sex-linked late feathering	V	Z	GGAZ
SLC45A2	*S*	Solute carrier family 45, member 2 (silver, gold, albinism plumage color)	V	Z	N/A [assembled on GGAZ]
LK	*lk*	Ladykiller	V	Z	N/A
LI	*Li*	Light down	V	Z	N/A

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
ABCA1	*y, Y*	ATP-binding cassette, subfamily A (ABC1), member 1 (sex-linked recessive white skin)	V	Z	N/A [assembled on GGAZ]
BR	*br*	Brown eye	V	Z	N/A
ID	*Id*	Dermal melanin inhibitor	V	Z	GGAZ
BARR	*B*	Barring dilution sex-linked feather pattern	V	Z	N/A
KO	*ko*	Head streak	V	Z	N/A
ALVE7	*ev7, ev-7, EV7*	Endogenous retrovirus 7 (defective ALV provirus)	V	Z	N/A [cytogenetically assigned to GGAZ]
ALVE21	*ev21, ev-21, EV21*	Endogenous retrovirus ev21	V	Z	GGAZ
BA	*ba*	Baldness, congenital	V	Z	N/A
CD	*cd*	Cerebellar degeneration	V	Z	N/A
CHOC	—	Chocolate plumage color, sex-linked	V	Not reviewed	N/A
CHZ	*chz*	Sex-linked chondrodystrophy	V	Z	N/A
CM	*cm*	Sex-linked coloboma	V	Z	N/A
DP4	*dp-4*	Diplopodia-4	V	Z	N/A
GA	*ga*	Gasper	V	Z	N/A
HZ	*H-Z*	Z-linked histoantigen	V	Z	N/A
J	*j*	Jittery	V	Z	N/A
POP	*pop*	Pop-eye	V	Z	N/A
PR	*pr*	Protoporphyrin inhibitor	V	Z	N/A
PW1	*Pw1*, Pw_1	Agglutinogen, pokeweed ("Pw1" agglutinogen)	V	Z	N/A
PW2	*Pw2*, Pw_2	Agglutinogen, pokeweed ("Pw2" agglutinogen)	V	Z	N/A
RG	*rg*	Recessive sex-linked dwarf	V	Z	N/A
SLN	*sln*	Sex-linked nervous disorder	V	Z	N/A

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
ST1	*St1*, St_1	Agglutinogen, potato ("St1" agglutinogen)	V	Z	N/A
ST2	*St2*, St_2	Agglutinogen, potato ("St2" agglutinogen)	V	Z	N/A
XL	*xl*	Sex-linked lethal	V	Z	N/A
Z	—	Dominant sex-linked dwarf	V	Z	N/A
—	*sex*	Sex-linked lethal Bernier	V	Z	N/A
HW	*H-W*	W-linked histoantigen	VI?	W (questionable assignment)	N/A
PPAT	*Ade-A*, *ADEA*, *GPAT*	Phosphoribosyl pyrophosphate amidotransferase (adenine synthesis A)	VII	6	N/A [linked to *ALB* and *PGM2* as shown by somatic cell hybridization; assembled on GGA4]
ALB	*Alb*	Albumin (serum preproalbumin)	VII	6	GGA4
GC	*Gc*, *VTDB*	Group-specific component (vitamin D-binding protein)	VII	6	GGA4
PGM2	*Pgm-2*, *RCJMB04_33e1*	Phosphoglucomutase 2	VII	6	N/A [linked to *ALB* and *PPAT* as shown by somatic cell hybridization; assembled on GGA4]
ADEB	*Ade-B*	Adenine synthesis B	VIII	7	N/A
DMD	*dys*	Dystrophin (muscular dystrophy, Duchenne and Becker types)	IX[d]	10	N/A [cytogenetically assigned to GGA10 but assembled on GGA1 sequence]
THRA	*c-erb-A*, *ERBA1*, *THRA1*	Thyroid hormone receptor, alpha [erythroblastic leukemia viral (v-erb-a) oncogene homolog, avian]	IX	Presumably chromosomes 10–14	N/A [assigned to a microchromosome by chromosomal fractionation; assembled on UN]

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
ETS1	*c-ets, c-ets-1, ETSB, MCW0075, LOC768354*	v-ets erythroblastosis virus E26 oncogene homolog 1 (avian)	IX	Presumably chromosomes 9–16	GGA24
FES	*c-fps, LOC429374*	Feline sarcoma oncogene	IX	Presumably chromosomes 9–16	N/A [assigned to a microchromosome by chromosomal fractionation; assembled on GGA10]
RAF1	*c-mil/mht, MIL*	v-raf-1 murine leukemia viral oncogene homolog 1	IX	Presumably chromosomes 9–16	N/A [assigned to a microchromosome by chromosomal fractionation; assembled on GGA12 sequence]
SRC	*c-src, MCW0050, SDR, PP60C-SCR*	v-src sarcoma (Schmidt-Ruppin A-2) viral oncogene homolog (avian)	IX	Presumably chromosomes 10–12	N/A [cytogenetically assigned to a microchromosome 10, 11 or 12; assembled on GGA20 sequence]
HCK	*ev3, ev-3, EV3, ALVE3, LOC419280*	Hemopoietic cell kinase (endogenous retrovirus 3)	IX	Microchromosome	GGA20
HPRT1	*hprt, HPRT*	Hypoxanthine phosphoribosyltransferase 1	IX	Microchromosome	GGA4
OVM	*Ovm, LOC416236, LOC396462*	Ovomucoid	IX	Presumably chromosomes 10–15	GGA13
TF	*Tf*	Transferrin (ovotransferrin, conalbumin)	IX	Presumably chromosomes 9–12	N/A [cytogenetically assigned to a microchromosome; assembled on GGA9 sequence]
TK1	*Tk-F, tk-F, TK*	Thymidine kinase 1, soluble (cytosol F)	IX	Microchromosome	N/A [assigned to a microchromosome by somatic cell hybridization; assembled on GGA18 sequence]
HBA1	*HBA, HBA@, HBAA*	Hemoglobin, alpha 1 (hemoglobin, alpha A)	IX	Presumably chromosomes 10–15	GGA14

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
HBA2	*HBAD, LOC416651*	Hemoglobin, alpha 2 (hemoglobin, alpha D)	IX	Presumably chromosomes 10–15	GGA14
HBZ	—	Hemoglobin, zeta (hemoglobin, pi and pi-prime; embryonic alpha-like globin)	IX	Presumably chromosomes 10–15	N/A [linked to *HBA1* and *HBAD*; assembled on GGA14 sequence]
HLA-B	*B@, MHC, HLA, LOC769497*	Major histocompatibility complex (MHC), class I, B	X	17	GGA16
MHCB	*B-G, Ea-B*	MHC B complex, class IV, B-G region	X	17	GGA16
HLA-G	*B-F, B-FL1, BF1, BF2, MHC1*	MHC B complex, class I, B-F region	X	17	GGA16
HLA-DRB5	*B-L, B-LBL2, B-LBL1, MHC2A, MHC2B, LOC425256*	MHC B complex, class II, B-L region	X	17	GGA16
CPBB	*Ea-B, EAB*	Erythrocyte alloantigen B (blood group system B)	X	17	GGA16
GAT	*Ir-GAT*	Immune response to synthetic polypeptide	X	17	N/A [GGA16 due to linking to *MHC*]
R-Rs-1	*Rs*	Subgroup C Rous sarcoma virus-induced tumor regression	X	17	N/A [GGA16 due to linking to *GAT*]
NOR	—	Nucleolar organizing region	X	17	N/A [GGA16 due to linking to *MHC*]
ACT	*act*	Macrophage activation	X	17	N/A [probably GGA16 due to linking to *MHC*]
ALVE(?)	*ev(?)*	ALV provirus	X	17	N/A [probably GGA16 due to linking to *MHC*]
EGFR	*c-erb-B, LOC396494*	Epidermal growth factor receptor [erythroblastic leukemia viral (v-erb-b) oncogene homolog, avian]	I, II, or IV?	2	GGA2
ALVE2	*ev2, ev-2, EV2*	Endogenous retrovirus 2 (codes for RAV-0)	I, II, or IV?	2	GGA1

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
SHL	*shl*	Shankless	I, II, or IV?	2	N/A [assigned to GGA2 based on an X-ray-induced pericentric inversion on 2p]
OV	*Ov, pUN121ov, LOC396058*	Ovalbumin	I, II, or IV?	2 or 3	GGA2
G(3)	*G_3, G3*	Egg white ovoglobulin G(3)	I, II, or IV?	2 or 3	N/A [probably GGA2 due to linking to *OV*]
MYC	*c-myc, CMYCA*	v-myc myelocytomatosis viral oncogene homolog (avian)	I, II, IV, or IX?	Presumably chromosomes 2, 3, or 13–16	GGA2
MYB	*c-myb, ROS0064*	v-myb myeloblastosis viral oncogene homolog (avian)	I, II, IV, or IX?	Presumably chromosomes 2, 3, or 13–16	GGA3
ACTB	*LOC396526, RCJMB04_4h19*	Actin, beta	I, II, IV, or IX?	Presumably chromosomes 2 or 9–12	N/A [cytogenetically assigned to GGA2; assembled on UN sequence]
ALVE14	*ev14, ev-14*	Endogenous retrovirus 14	I, II, or IV?	3	N/A [cytogenetically assigned to GGA3]
CPMM	*Ea-M, EAM*	Erythrocyte alloantigen M (blood group system M)	—	UN	N/A [linked to *CPQQ*]
CPQQ	*Ea-Q, EAQ*	Erythrocyte alloantigen Q (blood group system Q)	—	UN	N/A [linked to *CPMM*]
CPOO	*Ea-O, EAO*	Erythrocyte alloantigen O (blood group system O)	—	UN	N/A [linked to *CPSS*]
CPSS	*Ea-S, EAS*	Erythrocyte alloantigen S (blood group system S)	—	UN	N/A [linked to *CPOO*]
ES1	*Es-1*	Serum esterase 1	—	UN	N/A [presumably GGA2 due to linking to *ES2*]
ES2	*Es-2*	Serum esterase 2	—	UN	N/A [presumably GGA2 if controlled by *PON2*; linked to *ES1*]

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
IGY	*IgG-1, IGG*	Immunoglobulin 7S-1 IgG H chain	—	UN	GGA15
IGM	*IgM-1*	Immunoglobulin 17S-1 IgM H chain	—	UN	GGA15
TVA	*Tv-A, tva*	ALV subgroup A receptor	—	UN	GGA28
BTN1A1	*Tv-C, tvc, TVC*	Butyrophilin, subfamily 1, member A1 (ALV subgroup C receptor)	—	UN	GGA28
RHOBTB2	*Tv-B, TVBS3, CAR1, TVB*	Rho-related BTB domain containing 2 (cytopathic ALSV receptor; ALV subgroup B receptor)	—	UN	GGA22
TVE	*Tv-E, SEAR*	ALV subgroup E receptor	—	UN	N/A [GGA22 due to linking to *RHOBTB2*; assembled on GGA22 as *RHOBTB2*]
CHRND	—	Cholinergic receptor, nicotinic, delta	—	UN	N/A [assembled on GGA9; linked to *CHRNG*]
CHRNG	—	Cholinergic receptor, nicotinic, gamma	—	UN	N/A [assembled on GGA9; linked to *CHRND*]
LOC396498	*cryd1, CRYD1, d-cry*	Crystallin, delta 1	—	UN	N/A [assembled on GGA19; linked to *ALS*]
ASL	*cryd2, CRYD2*	Argininosuccinate lyase (crystallin, delta 2)	—	UN	N/A [assigned to GGA19 by RH mapping; assembled on GGA19; linked to *LOC396498*]
BL	*Bl*	Blue plumage color	—	Not reviewed	N/A [possibly GGA3 (if linked to *NA*), GGA1 (if controlled by *KITLG*) or GGA4 (if encoded by *KIT*)]
FM	*Fm*	Fibromelanosis	—	Not reviewed	N/A [possibly GGA11 due to linking to *MC1R* or GGA4 if controlled by *EDNRB2*]

(continued)

Table 9 (Continued)

Locus symbol[a]	Aliases	Locus/gene name (synonym)	Classical linkage group	Bitgood and Somes (1993) chromosome	Molecular linkage group according to Schmid et al. (2000, 2005) and other considerations[b]
TYR	*c*	Tyrosinase (oculocutaneous albinism IA) [autosomal albinism]	—	Not reviewed	GGA1

N/A, not assigned to the molecular map; UN, unknown chromosome or linkage group.

[a] According to Schmid et al. (2000, 2005). If possible and when there is a homologous human (or other mammalian) gene, the name of the homolog is used (Burt 1999)

[b] N/A, not assigned by molecular linkage mapping. Where applicable, chromosomal location of the genes in the whole-genome sequence assembly is given as found in the NCBI databases (http://www.ncbi.nlm.nih.gov/; accessed August 2006)

[c] There are several ptilopody loci, the one involved here has not been identified. Serebrovsky (1926) suggested at least two dominant and at least two recessive feathered shank genes. Somes (1992) described two loci, *PTI1* and *PTI2. PTI1* has two alleles, the Langshan allele (*PTI1***L*) and the Brahma allele (*PTI1***B*). The Brahma allele was shown to be dominant over the Langshan allele. Both the Sultan and Cochin breeds possess two shank-feathering loci, and one of the loci in the Sultan contained the *PTI1***L* allele. The comparable allele in the Cochin breed was hypothesized to be *PTI1***B*. The second locus in both of these breeds appears to be similar, and the symbol *PTI2* is suggested

[d] Discontinued. It was not a classical group, but was convenient for listing loci on microchromosomes (Bitgood and Somes 1990)

5.2.3 First Chicken Map

The first chicken genetic map was constructed by a Russian group led by A.S. Serebrovsky (Serebrovsky and Wassina 1927; Serebrovsky and Petrov 1928, 1930; Petrov 1931; Sungurov 1933). It was also the first linkage map ever developed for any domestic animal and, as such, was a great milestone in the history of genetics (reviewed by Romanov et al. 2004). Serebrovsky's group launched mapping of chicken genes in 1919 at the Central Station for Livestock Genetics, Anikovo. Serebrovsky and Petrov (1930) undertook one of the first attempts to summarize the available information on chicken linkage groups, six years before the article by FB Hutt (1936), but their work was overlooked or not properly credited by others (Moiseyeva et al. 2000; Romanov et al. 2004). The 1930 chicken map comprised four linkage groups with 12 genes and four other unlinked genes (Fig. 6) and was improved in two amendments published by Petrov (1931) and Sungurov (1933). Aggregated together, the map designed by Serebrovsky, Petrov, and Sungurov, with the acknowledged assistance of Serebrovskaya, Wassina, Rebrina, Kobystina, Ovsyannikova, and Grechka, included 15 chicken genes on six linkage groups: I, or Z chromosome (*ID-BARR-SLC45A2-K*), II (*CP-R*), III (*NA-BL*), IV (*LMBR1-D*), VI (*MC1R-FM*), and IX (*CR-SILV–F*), plus six independent loci (*P, APOA1, MB, TYR, PTI1*, and *PTI2*), and the recessive ptilopody gene*. The linkage group assignments or independent positions for these loci have been recently confirmed by molecular mapping (Sazanov et al. 1998; Okimoto et al. 1999; Pitel et al. 2000; Smith et al. 2000b, 2001a; Schmid et al. 2000; Kerje et al. 2003; Huang et al. 2006a).

These early linkage mapping efforts were supplemented by Dunn and Jull (1927), Warren (1928, 1933, 1935), Dunn and Landauer (1930), Jull (1930), Landauer (1931), Suttle and Sipe (1932), Hertwig (1933), Hutt (1933), Warren and Hutt (1936), and others. Hutt (1936) prepared the second map that consisted of 18 genes assigned to five linkage groups (Fig. 6). For some reason, Hutt did not provide any appropriate credit to the Serebrovsky and Petrov

*The numbering of true linkage groups (I–IV, VI, and IX) takes into account three independent loci (*P*, *APOAI*, and *MB*) that were also considered by Serebrovsky, Petrov, and Sungurov as single linkage groups V, VII, and VIII, respectively.

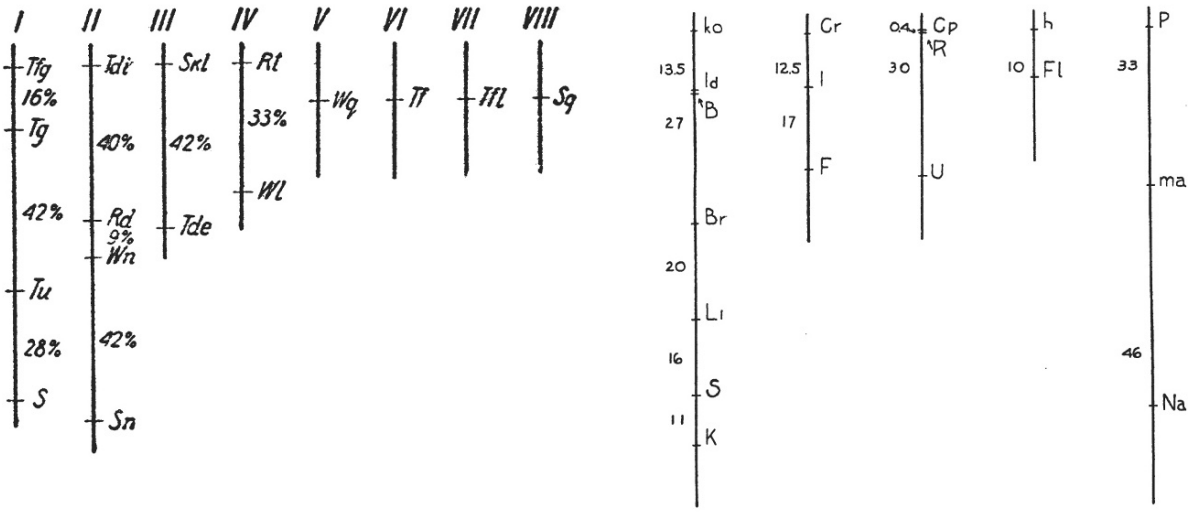

Fig. 6 The Serebrovsky and Petrov (1930) chicken chromosome map (*left*) based on the data obtained at the Central Station for Livestock Genetics, Anikovo by December 1, 1929, and the Hutt (1936) map (*right*). The genes on the Serebrovsky–Petrov map have been designated in accordance with Serebrovsky's own nomenclature (reviewed by Dunn 1928). The currently accepted locus symbols are given below in parentheses:
Linkage group I [GGAZ]: *Tfg (ID) — Tg (BARR) — Tu (SLC45A2) — S (K)*
Linkage group II: *Tdi (SILV)* [E22C19W28_E50C23 (classical group II)] — *Rd (CP)* [GGA4? (classical group I)] — *Wn (R)* [GGA4? (classical group I)] — *Sn (CR)* [E22C19W28_E50C23 (classical group II)]
Linkage group III: *Skl (NA)* [GGA3] — *Tde (BL)* [UN]
Linkage group IV [GGA2 (classical group IV)]: *Rt (LMBR1) — Wl (D)*
Chromosome V [GGA1]: *Wq (P)*
Chromosome VI [GGA11]: *Tf (MC1R)*
Chromosome VII [GGA24]: *Tfl (APOA1)*
Chromosome VIII [GGA1 or GGA24]: *Sq (MB)*

(1930) map, although aware of that study and even referring to it (Hutt 1933, 1936, 1949; Warren and Hutt 1936; Hutt and Mueller 1943). Hutt named his 1936 map the "first chromosome map" in subsequent publications (e.g., Hutt and Lamoreux 1940; Hutt 1949). The second map included three more loci (*KO, BR, LI*) on the sex chromosome, one more gene (*U*) linked to the *CP-R* group, one more gene (*ma*, which is now *DB*; Crawford 1990) linked to the *P* gene, and a new linkage group including *H* and *FL* (reviewed by Romanov et al. 2004). On the other hand, *P* and *NA* were located on the same chromosome in the Hutt (1936) map, which is now known not to be true, and did not include two Serebrovsky-Petrov-Sungurov linkage groups (*LMBR1-D* and *MC1R-FM*).

5.2.4 Subsequent Classical Mapping

The importance of genome maps of chicken and other domestic animals for understanding and utilizing the genetic foundations of these species has been acknowledged by both scientists and commodity groups (Romanov et al. 2004). In the 1920s and 1930s, the chromosome topography studies at the Anikovo Station were coordinated with egg production, growth, and other traits of economic values (Serebrovsky and Wassina 1927; Serebrovsky and Petrov 1928). Serebrovsky and Petrov (1930) proposed a "*signal gene*" concept, which is comparable to the modern notions of genetic marker and marker-assisted selection (MAS) (reviewed by

Romanov et al. 2004). The concept suggested that a signal gene does not affect an economic trait by itself. However, if located near a gene for an economic trait, it serves as a landmark for determining the latter. The accuracy of predicting such an association between the signal gene and the economic trait gene depends on the position of the signal gene relative to the trait gene, and the best prediction is achieved with two signal genes closely flanking the economic trait gene. Knowledge of a thorough chromosome map is a prerequisite for using the signal gene approach.

The Serebrovsky and Petrov (1930) and Hutt (1936) maps were further advanced by revisions of Hutt and Lamoreux (1940), Hutt (1949, 1960, 1964), Etches and Hawes (1973), Somes (1973, 1978, 1987), and Crawford (1990). The last update of the map (Bitgood and Somes 1993) listed 140 loci/traits including morphological mutations, biochemical polymorphisms, and chromosomal breakpoints (Romanov et al. 2004). Physical map positions were established for 41 single gene loci on five autosomal linkage groups and the Z chromosome (Tables 9 and 10). Moreover, there were 83 loci/traits assigned to one of the groups or chromosomes but without exact mapping information (including 25 loci/traits placed on microchromosomes), and eight pairs of linked markers are not anchored to a linkage group.

5.3 Molecular Genetics and Whole-Genome Sequence

5.3.1 First-generation Molecular Maps

In the 1990s, three reference mapping populations were developed for the chicken (reviewed by Romanov et al. 2004): the Compton population created at the Institute for Animal Health, UK (Bumstead and Palyga 1992); the East Lansing (EL) population developed at Michigan State University in collaboration with the United States Department of Agriculture (USDA) Avian Disease and Oncology Laboratory and the University of California at Davis, USA (Crittenden et al. 1993; Cheng et al. 1995); and the Wageningen University, Netherlands population (Groenen et al. 1998). The EL population involved 400 back cross (BC) progeny from two highly inbred lines, UCD001 (red junglefowl) and UCD003 (WL). The BC design maximized variation of the DNA markers to be mapped, so that each autosomal

Table 10 Breakdown of the updated classical gene map (Bitgood and Somes 1993) of the chicken

Classical linkage group	I	II	III	IV	V	VI	VII	VIII	X	IX[a]
Chromosome	GGA2, GGA3 or GGA4	GGA2, GGA3 or GGA4	GGA1	GGA2, GGA3 or GGA4	GGAZ	GGAW	GGA6	GGA7	GGA17 (now GGA16)	Other microchromosomes
No. of mapped loci	3	4	12	3	17	0	0	0	2	0
No. of assigned loci precisely not mapped[b]	13[c] (7)	See the table footnote c	23 (2) footnote c	See the table	21	1	4	1	8	17 (3)

[a] Discontinued (Crawford 1990)

[b] Numbers of loci assigned to more than one chromosome due to conflicting reports are given in parentheses

[c] Including three loci assigned to GGA2, one to GGA3, seven to more than one chromosome due to conflicting reports, and two to classical group I. If the two unmapped classical group I loci are ignored, the remaining 11 loci might equally belong to classical groups I, II, or IV. The chromosomes containing each of these linkage groups were unknown in 1993, but they were presumably GGA2, GGA3, and GGA4 (Bitgood and Somes 1993)

marker would be biallelic in the BC population. These three chicken linkage maps were integrated into one consensus map by Groenen et al. (2000). By that time, there were 1,965 loci localized on 26 chromosomes and 24 unknown linkage groups (Schmid et al. 2000). Further updates led to a map covering 4,200 cM with 2,261 loci on 53 linkage groups (Schmid et al. 2005). In many cases, smaller subsets of individuals were used to build the afore-mentioned reference maps (e.g., the EL map was based on genotypes for only 52 animals at most marker loci). The Wageningen mapping population included a larger set of animals (reviewed by Romanov et al. 2004).

Another chicken linkage map was developed using the Kobe University, Japan resource family (Lee et al. 2002). The integrated Hiroshima-Tsukuba map was also constructed in Japan using a resource population based on a cross between Japanese Game and White Leghorn chickens, and 301 markers, including 183 new ones, were localized to specific chromosomes either through linkage analysis or by analysis of the chicken draft sequence (Takahashi et al. 2005).

Initially, restriction fragment-length polymorphisms (RFLP) and random amplified polymorphic DNA (RAPD) markers with unknown sequence information were placed on the chicken genetic linkage map. Subsequently, microsatellites (or short tandem repeats), amplified fragment-length polymorphisms (AFLP), single nucleotide polymorphisms (SNP), and other sequence tagged site (STS) markers became the markers of choice. Mapped loci are subdivided in two classes: type I (coding sequences) and type II (anonymous, mainly microsatellites) markers. At present, 31 of the 53 linkage groups have been assigned to a particular chromosome (Masabanda et al. 2004). For the remaining 22 linkage groups, an ExxCxxWxx number is used with capital letters corresponding to the linkage groups of the original three linkage maps: East Lansing, Compton, and Wageningen (Schmid et al. 2005).

To map a mutant, experimental families segregating for one or more mutations are usually constructed (reviewed by Romanov et al. 2004). If no preliminary information of the chromosomal location of a mutant is available, a whole-genome scan using molecular markers is carried out (e.g., Lee et al. 2002). Bulked segregant analysis can essentially lower the cost of this approach (Michelmore et al. 1991; Ruyter-Spira et al. 1997, 1998; Pitel et al. 2000), where genotyping is done on DNA samples pooled according to the phenotype.

Currently, the positions of 62 classical mutants and loci have been determined based on linkage with molecular markers or localization using the whole-genome sequence assembly. There is one instance of discrepancy (the *DMD* locus) between the assembly data and linkage or physical mapping data (Table 9). The 78 classical loci/traits listed in Bitgood and Somes (1993) have to be assigned to the molecular map, not to mention many other reported classical mutations that have not yet been mapped. Only group I on the classical map that involves five mutations has not yet been connected with the molecular map. By analogy with the human and mouse short-limb disorders, the *FGFR3* gene mapped to GGA4 (Suchyta et al. 2001) might contain a causative mutation for the chicken creeper (*CP*), so the position of group I could be expected on this chromosome (Romanov et al. 2004). Mapping of the crest (*CR*) and frizzle (*F*) mutations that flank the dominant white mutation *(SILV)* on linkage group E22C19W28_E50C23 (Ruyter-Spira et al. 1997) would also facilitate the integration of molecular and classical maps (Schmid et al. 2000). A preliminary study by an Indian group (GB Pant University of Agriculture and Technology, http://gbpuat.ac.in/acads/cvsc/gnab.htm) demonstrated that the *F* gene is linked to *ROS0054* and *MCW0188* microsatellite loci on E22C19W28_E50C23. If there is a candidate gene for a mutation, it could be used to map the trait either by fluorescent in situ hybridization (FISH; e.g., Suzuki et al. 1999b) or by identification of a SNP within the gene (e.g., Dunn et al. 1999). Thus, the number of classical genes mapped with molecular markers is expected to increase.

Another approach for development of the genomic maps is the radiation hybrid (RH) panel (Brown et al. 2003). Whole-genome radiation hybrid (WGRH) panels can give higher resolution than conventional recombination analysis, and no polymorphisms are required for RH mapping. A chicken WGRH panel (ChickRH6) was created at Institut National de la Recherche Agronomique (INRA), France, by fusion of irradiated (6,000 rad) chicken embryonic fibroblasts and HPRT-deficient hamster cells (Morisson et al. 2002). The average retention rate of the chicken chromosomes was estimated as 21.9% in 90 clones, although it was lower than 20% for the two largest macrochromosomes.

An enormous collection of chicken ESTs that can be used for marker design and mapping have been generated making it the fourteenth most plentiful organism in the NCBI dbEST database (http://www.ncbi.nlm.nih.gov/dbEST/dbEST_summary.html; as of February 21, 2008). ESTs also serve as a source of information for identification of expressed genes and their function, and for annotating genome sequence and physical maps (Abdrakhmanov et al. 2000; Tirunagaru et al. 2000; Boardman et al. 2002; Brown et al. 2003).

5.3.2 Physical Maps

A clone-based physical map is built using contiguous, overlapping recombinant DNA clone inserts (contigs) that cover all, or almost all, of the genome (reviewed by Romanov et al. 2004). Contigs are often constructed by fingerprinting, which is done by digesting clones, such as BACs, with restriction enzymes. The resulting restriction patterns (or fingerprints) are then analyzed for shared fragments and overlapping clones are assembled into contigs. The integration of the genetic linkage map with the physical map provides the critical bridge between phenotypes, i.e., major mutations and quantitative trait loci (QTL), and their causative gene/allele combinations.

Since the mid-1990s, physical mapping resources have become readily available for major farm animal species including chicken. High-density large-insert libraries have been generated for the chicken and provide 4–10-fold genome coverage (Toye et al. 1997; Zimmer and Verrinder Gibbins 1997; Buitkamp et al. 1998; Crooijmans et al. 2000; Schmid et al. 2000; Kato et al. 2002). Using DNA from the UCD001 red junglefowl female 256 (Fig. 7), three BAC libraries have been produced in a collaboration between Texas A & M University and Michigan State University, USA (Lee et al. 2003). Based on the same UCD001 genome, another BAC library has been made at the Children's Hospital Oakland Research Institute (CHORI), CA, USA (Nefedov et al. 2003). Experimental chicken BAC libraries were also generated in Japan (Hori et al. 2000; Kato et al. 2002) and China (Liu et al. 2003b). These BAC libraries are publicly available (Table 11).

Many of these BAC libraries, including the four UCD001-based libraries and one derived from a WL chicken, have been used in physical mapping and genome sequencing projects (Crooijmans et al. 2000). BAC clones from these libraries were fingerprinted to build a physical contig map covering more than 90% of the chicken genome (Ren et al. 2003; Wallis et al. 2004). In parallel, a BAC-based whole-genome physical map of the chicken genome was integrated with the linkage map by hybridizing probes containing markers to filter-spotted arrays (Lee et al. 2003; Ren et al. 2003; Romanov et al. 2003).

Fig. 7 A female 256, the inbred red junglefowl line UCD001, served as a DNA source for generating BAC libraries and the draft sequence of the chicken genome. (Photograph courtesy of William S. Payne)

For integrating genetic and physical maps, a high-throughput screening technique is BAC filter hybridization using highly specific OVERGO probes (Romanov et al. 2003), which are overlapping oligo probes derived from specific sequence regions in known genes or markers. The OVERGO probes are synthesized by annealing two oligonucleotides that have an 8-bp overlap, followed by labeling in vitro. Use of OVERGOs facilitates pooling strategies because the melting temperatures for all probes are usually the same.

Typically, a collection of OVERGOs is arranged for three-dimensional screening by plates, rows, and columns. In the case of $6 \times 6 \times 6$ screening scheme, a set of 216 probes is designed, and a pool 36 OVERGOs is used for a single hybridization. Each probe

Table 11 Avian genomic BAC libraries

Species/breed (strain)/individual	Average insert size (kb)	No. of clones	Genome coverage	Vector	Cloning site	Country, library code (source's website or e-mail address)
Red junglefowl/inbred line UCD001/female #256	150	38,400	5.2×	pBeloBAC11	*Bam*HI	USA, 031-JF256-BI (http://hbz7.tamu.edu/homelinks/bac_est/bac.htm#animal)
Red junglefowl/inbred line UCD001/female #256	152	38,400	5.3×	pECBAC1	*Eco*RI	USA, 032-JF256-RI (http://hbz7.tamu.edu/homelinks/bac_est/bac.htm#animal)
Red junglefowl/inbred line UCD001/female #256	171	38,400	6.0×	pECBAC1	*Hin*dIII	USA, 033-JF256-H3 (http://hbz7.tamu.edu/homelinks/bac_est/bac.htm#animal)
Red junglefowl/inbred line UCD001/female #256	195	73,700	12.0×	pTARBAC2.1	*Eco*RI	USA, CHORI-261 (http://bacpac.chori.org/chicken261.htm)
Chicken/White Leghorn/a female	130	49,920	5.4×	pECBAC1	*Hin*dIII	USA, The Netherlands, 020-CHK-H3 (http://hbz7.tamu.edu/homelinks/bac_est/bac.htm#animal; http://www.geneservice.co.uk/products/clones/chicken_BAC.jsp)
Chicken/White Leghorn (Julia line)/a female embryo	149	49,152	3.2×	pBAC-Lac	*Hin*dIII	Japan, N/A (s-mizuno@brs.nihon-u.ac.jp)
Chicken/White Silkie/a female	118	138,240	13.34×	pBeloBAC11	*Hin*dIII	China, N/A (ninglbau@public3.bta.net.cn)
Turkey/inbred line, Nicholas Turkey Breeding Farms/a female	190	71,000	11.1×	pTARBAC2.1	*Eco*RI	USA, CHORI-260 (http://bacpac.chori.org/turkey260.htm)
Duck	117.94	84,480	9.84×	pIndig-5	*Hin*dIII	China, N/A (ninglbau@public3.bta.net.cn)
Emu	165	133,632	13.5×	pCCBAC1E	N/A	USA, VMRC16 (http://www.benaroyare-search.org/investigators/amemiya_chris/libraries.htm)
Zebra finch	134	147,456	15.5×	pCUGIBAC1	*Hin*dIII	USA, TG_Ba (http://www.genome.arizona.edu/orders/direct.html?library=TG_Ba)
California condor/female "Molloko" (Studbook #45)	N/A	89,665	~14×	pTARBAC2.1	*Eco*RI	USA, CHORI-262 (http://bacpac.chori.org/library.php?id=222)

N/A, not available

can be assigned to a number of positive BAC clones common for a particular intersection of plate, row, and column (Romanov et al. 2003).

Screening of the four UCD001 BAC libraries identified 918 genes and markers across all chromosomes and linkage groups, resulting in assignments of nearly 8,000 clones. Most of the OVERGOs were single copy in the chicken genome and the resulting assignments are available online (U.S. Poultry Genome Project http://poultry.mph.msu.edu/resources/Resources.htm#bacdata) and contributed to the alignment of the first-generation BAC-contig map (Ren et al. 2003) to the linkage map (Fig. 8). They also aided in alignment of the second-generation physical map to the linkage map (Wallis et al. 2004), developed in parallel with the whole-genome sequence, and resulted in the assignment of BAC contigs to specific chicken chromosomes (Fig. 9). The second-generation physical map was made at 20-fold coverage and contained 260 contigs of 180,000+ overlapping clones. It covers about 91% of the chicken genome and has been used for determining chicken BACs aligned to positions in other sequenced genomes (Wallis et al. 2004).

Additionally, the physical map has been integrated with the cytogenetic map. Many BACs positive for genes have been hybridized by FISH to several chicken chromosomes (e.g., Sazanov et al. 2004a, b; Fig. 10), and a detailed analysis of microchromosome 17 using FISH has been conducted (Romanov et al. 2005). The GGA17 map orientation was demonstrated to be different and reversed from that currently proposed for the linkage map and draft sequence.

5.3.3 Whole-Genome Sequence

Over the previous 100 years of chicken genetics, efforts have been aimed at genetic mapping in order to identify, characterize, and locate genes associated

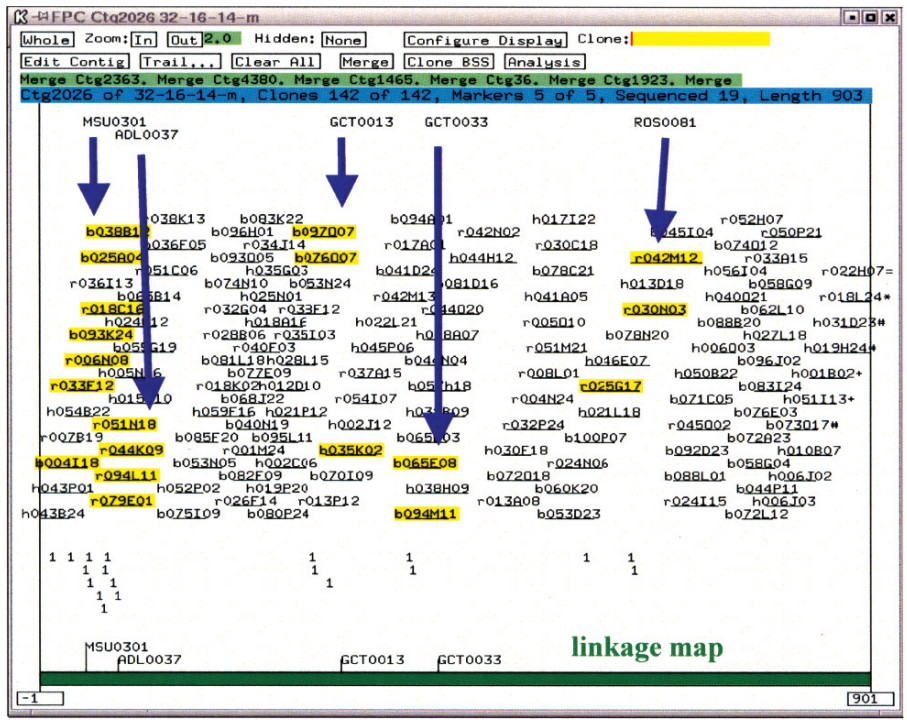

Fig. 8 First-generation BAC physical map of the chicken genome (after Ren et al. 2003). Example of a BAC contig anchored to the GGA1 genetic map. This contig consists of 142 clones from three source BAC libraries (prefixed with "h," "b," and "r"), contains 903 unique fingerprint bands, and is estimated to span 4.01 Mb. The contig was anchored to the region around 361 cM of the GGA1 genetic map using five DNA markers, *MSU0301, ADL0037, GCT0013, GCT0033*, and *ROS0081* (Groenen et al. 2000) as shown with the arrows. The highlighted clones indicate the positive clones identified by DNA marker hybridization

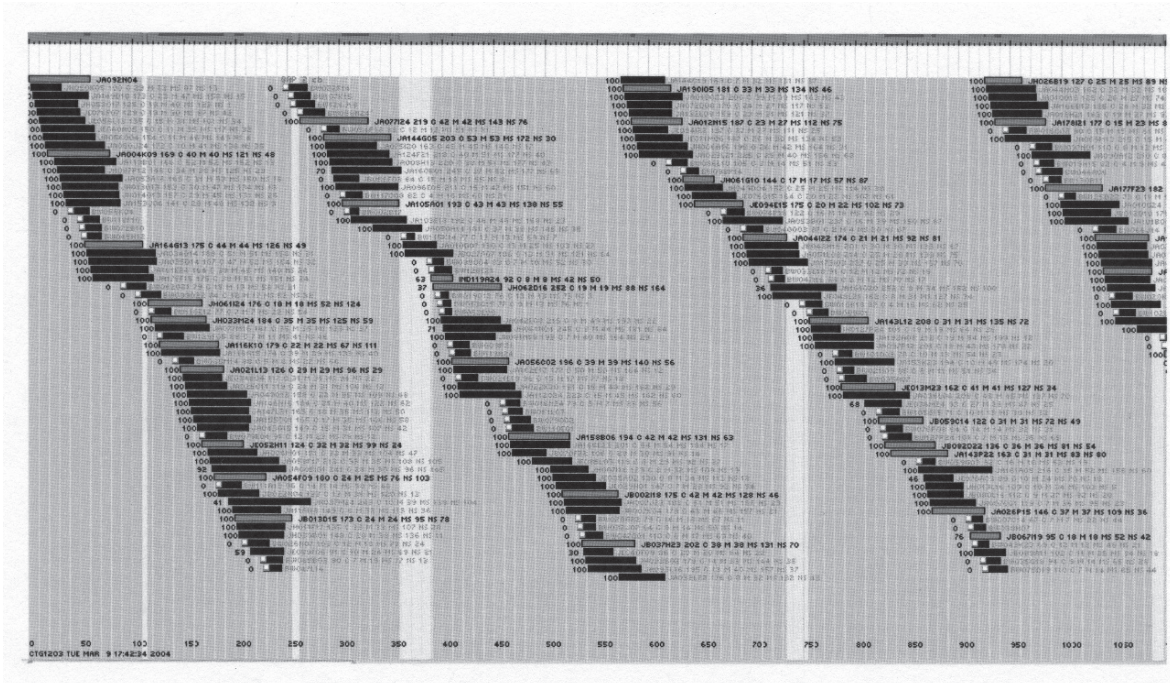

Fig. 9 Chicken BAC tiling set from the fingerprint map for, List 003, Ctg 1203 (Martin Krzywinski, Genome Sciences Centre, Vancouver, Canada). The estimated minimum tiling path set consisted of 9,210 BAC clones with an average clone overlap of 77 kb (Wallis et al. 2004)

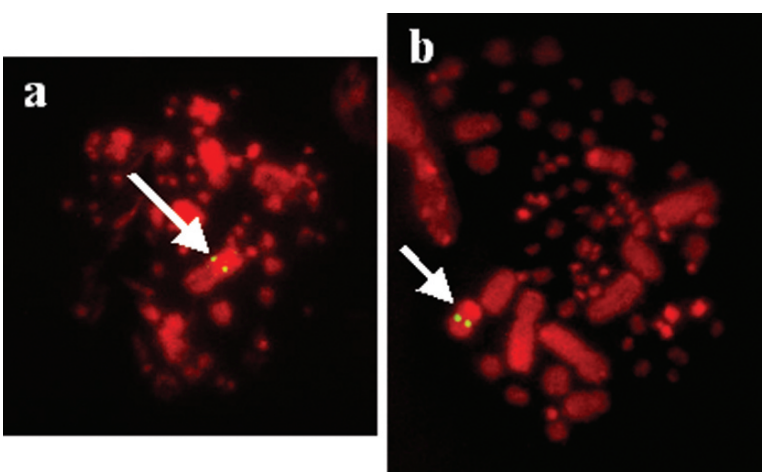

Fig. 10 FISH of the chicken BAC clones. (**a**) Clone b071F17 (*KITLG*, GGA1; Sazanov et al. 2004a). (**b**) Clone b027G23 (*CTSL*, GGAZ; Sazanov et al. 2004b; *arrows* indicate sites of specific hybridization)

with productivity and health of the species (Romanov et al. 2004). To elucidate genomic architecture underlying productivity and disease resistance traits, further progress in chicken gene discovery and, eventually, the complete genome sequence will be required. The whole-genome sequence is the ultimate physical map and the basis for a high-resolution linkage map (Dodgson 2003).

In February 2002, a "white paper" for sequencing the chicken genome was submitted to the US National Human Genome Research Institute (NHGRI). The proposal stated that because of its evolutionary distance from mammals (around 310 MYA), the chicken would make a significant contribution to comparative genomics at the sequence level. Due to a notable level of conservation in gene order between mammalian

and chicken genomes, the chicken genome is also a perfect model for studying the evolution of gene order and arrangement (Burt et al. 1999; Groenen et al. 2000; Waddington et al. 2000; Suchyta et al. 2001). The NHGRI added the chicken to the list of high-priority genomes for sequencing, making it the first sequenced bird genome and also the first sequenced agricultural species (Jensen 2005). The project objectives were to provide the assembly of a 6-fold whole-genome shotgun coverage of the UCD001 genome and ordered the resulting sequence scaffolds by alignment to BAC, fosmid, and plasmid-paired end reads in a comprehensive contig map at the Washington University Genome Sequencing Center (WUGSC, St. Louis, MO, USA) (reviewed by Romanov et al. 2004). This strategy led to a high-quality assembly thanks to the relatively small size of the chicken genome (1/3 that of a mammal) and low repetitive DNA content (only 11% compared with 40–50% in mammals) (Burt 2005).

The approximately 1 Gigabase sequence published in *Nature* by the International Chicken Genome Sequencing Consortium (2004) is based on DNA from the inbred red junglefowl female 256. At a later stage, gaps in the genome sequence should be finished and errors eliminated in the contig assembly. In particular, a substantial number of clone contigs have unknown or ambiguous chromosome assignment (Aerts et al. 2005). As a contribution to the assembly, Aerts et al. (2005) mapped 86 SNP markers derived from 86 clones on the genetic map and, thus, anchored 56 clone contigs and 13 individual BACs that correspond to a total of 57,145 clones. Another problem is a poor assembly of the sex chromosome sequences, which currently contains only 30% of the Z [expected 100 Megabases (Mb)] and 2% of the W (expected 30 Mb) chromosomes, due to single copies of these chromosome in the female used for sequencing as well as high repeat content in the W chromosome. Owing to overlaps with an additional set of BACs sequenced to high quality, sequence coverage on the autosomes was 98% (Burt 2005). The sequence was only obtained for 30 chromosomes, although the final goal is to have linkage and sequence maps for all 39 chromosomes in the chicken genome (Schmid et al. 2005).

The draft sequence is also being annotated in terms of aligning and characterizing genes and other genome elements. Overlaps with cDNA clones suggested 5–10% of genes were missing from the final assembly because of gene duplications (e.g., MHC region) and GC-rich sequences (Burt 2005). The sequence annotation will eventually contain an estimate of 20,000–23,000 chicken genes (International Chicken Genome Sequencing Consortium 2004).

Advanced bioinformatics resources involving genome browsers, genetic maps, marker and gene expression databases, and other related poultry genetics and genomics information are available on the World Wide Web (see the selected list at the end of this chapter).

5.3.4 Chicken Genome and Sequence Features

Birds are characterized by the greatest conservatism of genome size among vertebrate animals, with the diploid nuclear DNA content per nucleus ranging between 2.5 and 3.0 picograms (1 pg = 978 Mb) (as reviewed by Romanov et al. 2004). Haploid DNA content (C value) for various avian species, including the chicken, is presented in Table 8. The average avian haploid genome is 1.45 pg; flightless birds have larger genome sizes, with the largest one being 2.16 pg in the ostrich. The chicken genome is at 2.8-fold less than the average mammalian genome (Gregory 2006).

The size of the avian genome positively correlates with red blood cell and nucleus sizes and negatively with metabolic rate. There is no correlation with developmental rate or longevity, and no cases of polyploidy in birds are known. Comparatively low DNA content could be because of the "necessity of flight," i.e., as a response to selection for high metabolism/flight, or due to high evolutionary conservatism of this parameter, taking into consideration monophyletic origin of the class *Aves* (Kadi et al. 1993; Gregory 2006).

The avian karyotype is characterized by a remarkably large number and heterogeneity of chromosomes. The avian karyotype contains several macrochromosomes (3–8 m) and numerous microchromosomes (0.3–3 m) (Schmid et al. 2000). The chicken karyotype is thought to represent an ancestral type of avian karyotype (Rodionov 1997; Derjusheva et al. 2004).

In the past, the number of macrochromosomes varied in the literature between 6 and 10 pairs, including the Z and W in the heterogametic female (Schmid et al. 2005). The International Chicken Genome

Sequencing Consortium (2004) designated three chromosome size groups: large macrochromosomes (GGA1–5), intermediate chromosomes (GGA6–10), and 28 microchromosomes (GGA11–38). Masabanda et al. (2004) and Schmid et al. (2005) proposed a new, definitive classification system. In accordance with this classification, group A is composed of chromosomes 1–10, Z, and W (cytogenetically distinguishable macrochromosomes tractable in a flow karyotype). Group B is composed of chromosomes 11–16 (large microchromosomes up to and including the nucleolar organizing region chromosome). Group C is composed of chromosomes 17–32 (small microchromosomes most of which associated with known linkage groups) and group D chromosomes 33–38 (smallest microchromosomes not yet associated with known linkage groups).

Chicken microchromosomes constitute about 23% of the genome and possess not less than 50% of the avian genes (Smith et al. 2000b; Schmid et al. 2000). Furthermore, there are many indirect indications of the increased gene density on the microchromosomes (e.g., Andreozzi et al. 2001; Habermann et al. 2001). The recombination frequencies in macro- and microchromosomes are one crossover per 30 and 12 megabases (Mb), respectively, which is two and five times less than in mammals (Rodionov 1996). Detailed elaboration of the structural and functional organization of chicken microchromosomes would be useful for both enlightening minimally required elements of eukaryotic chromosomes and studying the evolution of vertebrate karyotypes (Romanov et al. 2004).

As a result of the comparative genomics analysis, 80 or more regions of evolutionary conservation have been suggested on the aligned human and chicken chromosomes (Burt et al. 1999; Burt 2002). This level of conserved grouping of orthologous genes, also called conserved synteny ("gene loci in different organisms located on a chromosomal region of common evolutionary ancestry"; Passarge et al. 1999), was even higher than that between the human and the mouse (Burt et al. 1999).

As a straightforward approach for direct physical mapping, FISH of chicken chromosomes is normally used. The intrachromosomal localization has been identified for around 250 type I markers (reviewed by Romanov et al. 2004). Moreover, many cytogenetically assigned large-insert clones that include coding sequences can be employed for comparative genome anchoring. There are a number of FISH techniques for determining hybridization signals that are used for chicken genome mapping. Using large-insert clones of genomic libraries like BACs as DNA probes for FISH achieves almost 100% efficiency of hybridization, making it one of the most perspective approaches (Buitkamp et al. 1998; Smith et al. 2000b; Sazanov et al. 2002). Sets of chromosome-specific clones and whole chromosome paints represent powerful tools for microchromosome detection and ordering (Zimmer et al. 1997; Fillon et al. 1998; Guillier-Gensik et al. 1999). To improve the resolution of FISH technique, lampbrush chromosomes, in addition to mitotic ones, can be effectively used (Mizuno and Macgregor 1998; Rodionov et al. 2002). Using the confocal microscopy, spatial distribution of the chromosome paints in the chicken nucleus can be examined to better understand micro- and macrochromosome localization features during interphase (Habermann et al. 2001). Chromosome microisolation and microcloning followed by isolation and mapping of microsatellite markers is another approach for increasing map density (Ambady et al. 2002). The combination of molecular and cytological approaches was demonstrated in a study of the W chromosome by Itoh and Mizuno (2002).

Ultimately, the 6.6-fold coverage draft genome sequence was generated and its analysis revealed the following major features (International Chicken Genome Sequencing Consortium 2004):

- The chicken genome is characterized by a substantial decrease in interspersed repeat content, pseudogenes and segmental duplications, and in intron size. This reduction accounts for the nearly 3-fold difference in size between the chicken and mammalian genomes.
- There are long blocks of conserved synteny that contain chicken–human aligned segments (Fig. 11).
- When comparing macro- vs. microchromosomes, there is a negative correlation between the size of chicken chromosomes and recombination rate (Fig. 12), G + C and CpG content, and gene density, but there is a positive correlation between chromosome size and repeat density.
- Genes in both chicken microchromosomes and in subtelomeric regions of macrochromosomes show higher synonymous substitution rates.

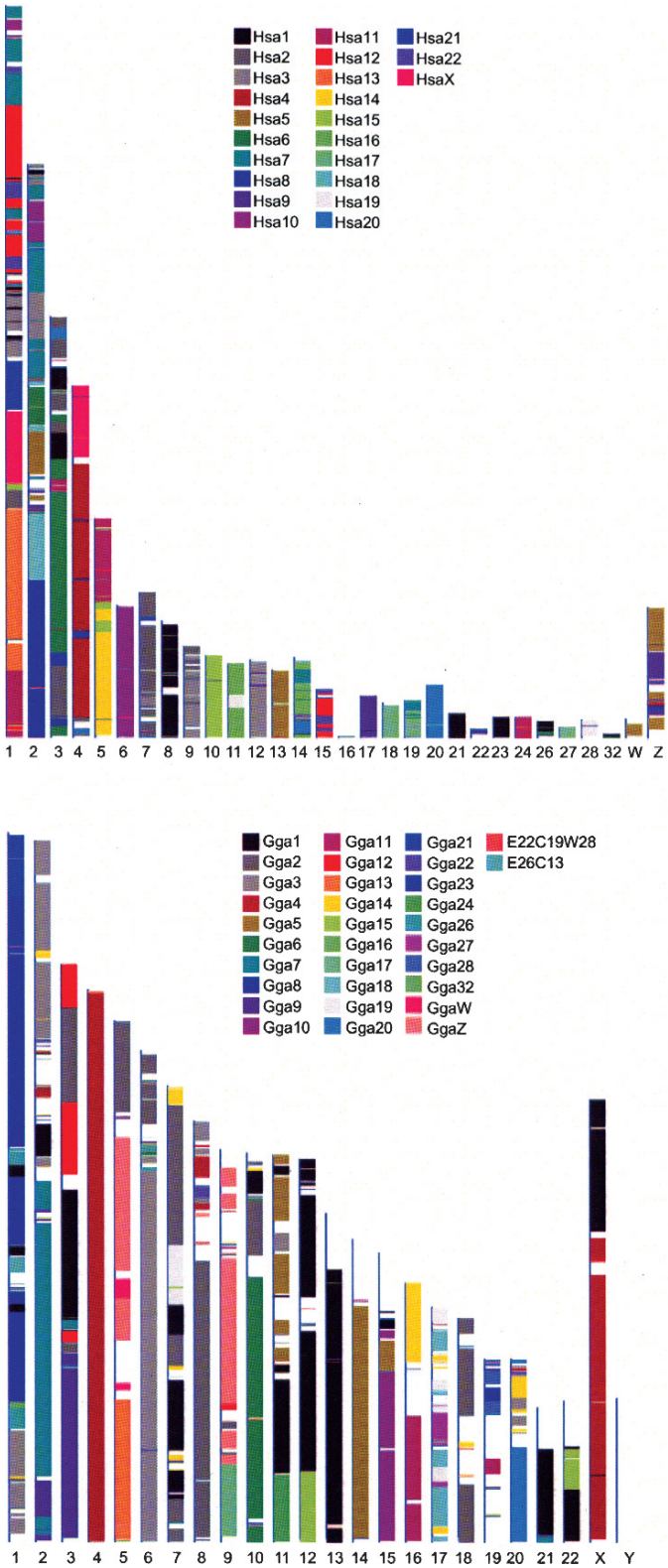

Fig. 11 Maps of conserved synteny between chicken chromosomes and human chromosomes (reprinted with permission from Macmillan Publishers Ltd: Nature, International Chicken Genome Sequencing Consortium 2004, © 2004): chicken compared to human (*top*), and human compared to chicken (*bottom*)

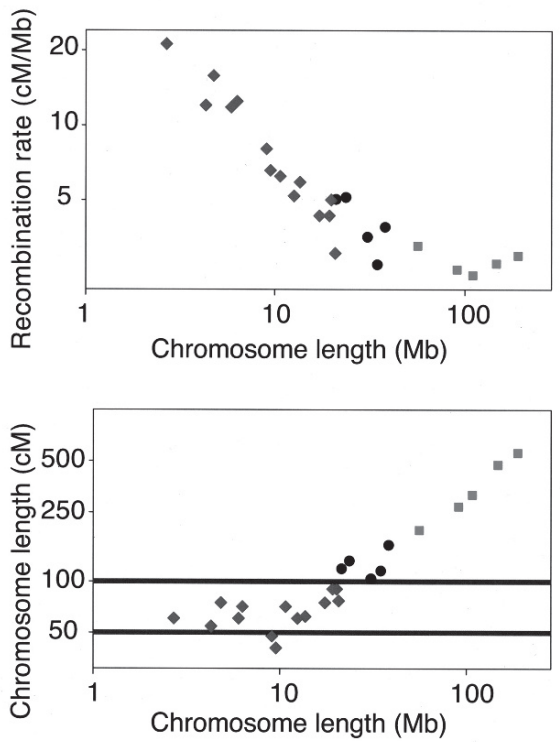

Fig. 12 Relationships between chicken chromosome characteristics for chromosomes 1–28: comparison of recombination rate and sequence length (*top*), and comparison of genetic and sequence length (*bottom*). Both plots exclude chromosomes 16, 22, 23, 25, which have insufficient genetic markers or sequence. *Upright squares*: macrochromosomes; *circles*: intermediate chromosomes; *diagonal squares*: microchromosomes (adapted with permission from Macmillan Publishers Ltd: Nature, International Chicken Genome Sequencing Consortium 2004, © 2004)

- Unlike other vertebrate genomes, the chicken genome has had no active insertions of short interspersed nucleotide elements (SINE) over the last 50 MYR.
- At least 70 Mb of the chicken–human aligned sequences seem to be functional in both species.
- Alignment of the chicken–human noncoding sequences often led to their localization far from genes and in clusters that are likely to be under selection for unknown functions.

In a parallel article, the International Chicken Polymorphism Map Consortium (2004) described 2.8 million SNPs that represented the first chicken genome-wide genetic variation map. This set of SNPs was designed by comparing the sequences of three domestic chicken breeds (a broiler, a layer, and a Chinese Silkie) and the red junglefowl. At least 90% of the variant sites were true SNPs, and at least 70% were common SNPs showing segregation in many domestic breeds. For almost every possible comparison between domestic breeds and junglefowl, average nucleotide diversity was about five SNPs per 1 kilobase (kb), which contradicts with previous views of domestic animals as highly inbred in comparison with their wild progenitors. Most of the chicken SNPs seem to have arisen prior to domestication, and little evidence of selective sweeps for adaptive alleles was found on length scales greater than 100 kb.

The chicken genome sequence and genetic polymorphisms are expected to benefit agriculture and medicine, shed new light on animal domestication, and provide an ideal model for studies in development and evolution as well as comparative research in 9,600 extant avian species (Burt 2005).

5.3.5 Genetics and Molecular Mapping in Other Birds

Until recently, genetic studies and gene mapping in the other poultry, semidomesticated and caged species (Table 1) have been carried out at a significantly slower pace despite the fact that duck, Muscovy duck, canary, pigeon and budgerigar, along with chicken, mouse, rat, rabbit, and three fish species, were among the first vertebrates in which sex-linked and autosomal-linked genes were found (Durham and Marryat 1908; Spillman 1908; Hutt 1936; Table 12). The limited classical linkage maps of the Japanese quail and turkey Z chromosome involved only two and three morphological loci, respectively (Crawford 1990; Minvielle et al. 2000). There were also four known classical Z-linked loci in the turkey, five in the ring-necked pheasant, three in the guinea fowl, three in the peafowl, five in the pigeon, one in the African collared dove, four in the domestic duck, two in the Muscovy duck, one in the mute swan and, presumably, up to five in the goose (Table 12). Additionally, four classical autosomal linkage relationships have been reported in the Japanese quail, two in each of the turkey and dove, and one in each of the duck and pigeon. Several cases of sex and autosomal linkage have been discovered in major caged birds.

Table 12 Linkage in other avian species raised by man

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
		Anseranser (goose)	
b	Diluted feet	Z	Staško (1970)
b^1	Buff celler	Z	Hollander (1990)
G	Gray	Z (linked to *Sd*)	Crawford (1990)
Sd	Dilution	Z (linked to *G*)	Crawford (1990)
Sp^2	Solid pattern	Z	Crawford (1990)
		Cygnusolor (muteswan)	
r	Polish	Z	Lancaster (1977)
		Cairina moschata (Muscory duck)	
ALDOB	Aldolase B, fructose-bisphosphate	Z	Nanda and Schmid (2002)
ch^3	Chocolate	Z	Sokolovskaya (1935); Hollander (1970); Crawford (1990)
—	Crest	Z	Sokolovskaya (1935)
HBA1	Hemoglobin, alpha 1 (globin, alpha A)	AL (linked to *HBA2* and *HBAZ*)	Niessing et al. (1982); Erbil and Niessing (1984)
HBA2	Hemoglobin, alpha 2 (globin, alpha D)	AL (linked to *HBA1* and *HBAZ*)	Niessing et al. (1982); Erbil and Niessing (1984)
HBAZ	Hemoglobin, zeta (embryonic alpha-globin pi-prime)	AL (linked to *HBA1* and *HBA2*)	Niessing et al. (1982); Erbil and Niessing (1984)
HBG1	Hemoglobin, gamma A (globin, epsilon)	AL (linked to *HBG2*)	Lin and Paddock (1984)
HBG2	Hemoglobin, delta (globin, beta)	AL (linked to *HBG1*)	Lin and Paddock (1984)
		Anas platyrhynchos (domestic duck) Buff dilution	
bu		Z	Crawford (1990)
d^3	Brown dilution	Z	Crawford (1990)
IFNA1	Interferon, alpha 1	Z	Nanda et al. (1998)
IFNB1	Interferon, beta 1, fibroblast	Z	Nanda et al. (1998)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	Hori et al. (2000)
ASL <CRYD2>	Argininosuccinate lyase (crystallin, delta 2)	AL (linked to *CRYD1*)	Li et al. (1995)
CRYD1<d-cry>	Crystallin, delta 1	AL (linked to *ASL*)	Li et al. (1995)
E	Black	AL (linked to *S*)	Crawford (1990)
HLA-B	MHC, class I, B	AL (linked to *TAP2*)	Mesa et al. (2004)
S	Bib	AL (linked to *E*)	Crawford (1990)
TAP2	Transporter 2, ATP-binding cassette, subfamily B (MDR/TAP)	AL (linked to *HLA-B*)	Mesa et al. (2004)

(continued)

Table 12 (Continued)

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
	Meleagris gallopavo (turkey) Achondroplasia		
ach		Z	Crawford (1990)
bo	Bobber	Z	Crawford (1990)
e	Brown	Z	Crawford (1990)
K	Late feathering	Z	Crawford (1990)
n (n, n^{al})	Narragansett, imperfect albinism	Z	Crawford (1990)
tt	Tetanic torticollar spasm	Z	Savage et al. (1993)
vi	Vibrator	Z	Crawford (1990)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	Hori et al. (2000)
D	Slate	AL (linked to *ga*)	Crawford (1990)
ga	Glaucoma	AL (linked to *D*)	Crawford (1990)
ha	Hairy	AL (linked to r)	Crawford (1990)
r	Red	AL (linked to *ha*)	Crawford (1990)
	Pavo cristatus (Indian peafowl)		
ca <d>	Cameo (silver-dun)	Z	Somes and Burger (1988); Hollander (1990)
—	Purple	Z	Legg[4]
—	Peach	Z	Legg[4]
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	Hori et al. (2000)
a	*Phasianus colchicus* (ring-necked pheasant) Incomplete albinism	Z	Crawford (1990)
Ba	Barring	Z	Crawford (1990)
di	Dilute	Z	Crawford (1990)
DMRT1	Doublesex and mab-3-related transcription factor 1	Z	Nanda et al. (2000)
id	Dermal melanin	Z	Crawford (1990)
s	Gold	Z	Crawford (1990)
	P. versicolor (green pheasant)		
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	Hori et al. (2000)
	Chrysolophus pictus (golden pheasant)		
ALDOB	Aldolase B, fructose-bisphosphate	Z	Nanda and Schmid (2002)

(continued)

Table 12 (Continued)

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
DMRT1	Doublesex and mab-3-related transcription factor 1	Z	Nanda et al. (2000)
	Coturnix coturnix (common quail)		
DMRT1	Doublesex and mab-3-related transcription factor 1	Z	Nanda et al. (2000)
	C. japonica (Japanese quail)		
ACO1 <IREBP>	Aconitase 1, soluble	Z	Saitoh et al. (1993)
ALDOB	Aldolase B, fructose-bisphosphate	Z	Suzuki et al. (1999a), Nanda and Schmid (2002)
SLC45A2 <AL (al, al^{C}, al^{D}, al^{reb})>	Solute carrier family 45, member 2 (imperfect albino, cinnamon, dark-eyed dilute, red-eyed brown)	Z	Crawford (1990); Minvielle et al. (2000); Gunnarsson et al. (2007)
BR (br, ro)	Brown, roux	Z	Crawford (1990); Minvielle et al. (2000)
EMB <ZOV3>	Embigin homolog (mouse)	Z	Saitoh et al. (1993)
GHR	Growth hormone receptor	Z	Suzuki et al. (1999a)
MUSK	Muscle, skeletal, receptor tyrosine kinase	Z	Suzuki et al. (1999a)
PRLR	Prolactin receptor	Z	Suzuki et al. (1999a)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	Hori et al. (2000)
Bh	Black at hatch	1	Niwa et al. (2003)
ALB <Alb>	Albumin	AL (linked to s and *GC*)	Crawford (1990); Shibata and Abe (1996)
GC	Group-specific component (vitamin D-binding protein)	AL (linked to *ALB*)	Shibata and Abe (1996)
EDNRB2 <S>	Endothelin receptor B subtype 2 gene (panda)	AL (linked to *ALB*)	Crawford (1990); Miwa et al. (2006, 2007)
E	Extended brown	AL (linked to *GPI*)	Crawford (1990)
GPI <Pgi>	Glucose phosphate isomerase	AL (linked to *E*)	Crawford (1990)
HIST1H1A <H1.a>	Erythrocyte histone H1.a	AL (linked to *HIST1H1B* and *HIST1H1Z*)	Palyga (1998)
HIST1H1B <H1.b>	Erythrocyte histone H1.b	AL (linked to *HIST1H1A* and *HIST1H1Z*)	Palyga (1998)
HIST1H1Z <H1.z>	Erythrocyte histone H1.z	AL (linked to *HIST1H1A* and *HIST1H1B*)	Palyga (1998)
wb	White-breasted	AL (linked to *y*)	Crawford (1990)
y	Yellow	AL (linked to *wb*)	Crawford (1990)

(continued)

Table 12 (Continued)

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
	Numida meleagris (guinea fowl)		
ACO1 <*Acon*^{B}>	Aconitase 1, soluble (cytoplasmic aconitase)	Z	Crawford (1990)
is	Brown, dundotte	Z	Hollander (1990)
k	Sex-linked feathering	Z	Crawford (1990)
	Serinus canaria (island canary)		
cin	Cinnamon (brown)	Z	Mason[5]
ino (ino, ino^{ag})	Sex-linked imperfect albinism, agate	Z	Durham and Marryat (1908); Onsman[6]
—	Hearing and song in the Belgian Waterslager canary	Z	Wright et al. (2004)
	Taeniopygia guttata (zebra finch)		
ACO1 <*IREBP*>	Aconitase 1, soluble	Z	Lacson and Morizot (1988), Itoh et al. (2006)
ATP5A1	ATP synthase, H+ transporting, mitochondrial F1 complex, alpha subunit 1, cardiac muscle	Z	Itoh et al. (2006)
B	Brown (fawn)	Z	Miller (1992)
C	Chestnut flanked white	Z	Miller (1992)
CHD1	Chromodomain helicase DNA-binding protein 1	Z	Itoh et al. (2006)
DMRT1	Doublesex and mab-3-related transcription factor 1	Z	Itoh et al. (2006)
GHR	Growth hormone receptor	Z	Itoh et al. (2006)
HINT1	Histidine triad nucleotide-binding protein 1	Z	Itoh et al. (2006)
HSD17B4	Hydroxysteroid (17-beta) dehydrogenase 4	Z	Itoh et al. (2006)
NIPBL	Nipped-B homolog (Drosophila)	Z	Itoh et al. (2006)
NR2F1	Nuclear receptor subfamily 2, group F, member 1	Z	Itoh et al. (2006)
NTRK2	Neurotrophic tyrosine kinase, receptor, type 2	Z	Chen et al. (2005), Itoh et al. (2006)
PAM	Peptidylglycine alpha-amidating monooxygenase	Z	Itoh et al. (2006)
S	Silver	Z	Miller (1992)
SMAD2	SMAD family member 2	Z	Itoh et al. (2006)
SPIN1	Spindlin 1	Z	Itoh et al. (2006)
UBE2R2	Ubiquitin-conjugating enzyme E2R 2	Z	Itoh et al. (2006)

(continued)

Table 12 (Continued)

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
—	Light back	Z	Miller (1992)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	O'Neill et al. (2000)
	Columba livia (pigeon)		
ACO1 <IREBP>	Aconitase 1, soluble	Z	Saitoh et al. (1993)
b (B^A, *b*)	Ash-red, brown	Z	Hollander (1990)
d (D^p, *d*)	Pale, dilute	Z	Hollander (1990)
EMB <ZOV3>	Embigin homolog (mouse)	Z	Saitoh et al. (1993)
R (*r*, r^{RU})	Reduced, rubella	Z	Hollander (1990); Huntley[7]
St (*St*, St^H, St^Q, St^F, St^{Sa}, St^{Fr}, St^C)	Almond, hickory, qualmond, faded, sandy, frosty, chalky	Z	Hollander (1990); Huntley[7]
Wl	Web lethal	Z	Hollander and Miller (1982); Hollander (1990)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	Hori et al. (2000)
C (C^T, C^D, *C*, C^L, *c*)	T-pattern, dark checker, checker, light checker, barless	AL (linked to *o* and *S*)	Miller and Hollander (1978); Huntley[7]
o	Opal	AL (linked to *C* and *S*)	Miller and Hollander (1978); Huntley[7]
S	Spread pattern	AL (linked to *C* and *o*)	Miller and Hollander (1978); Huntley[7]
	Streptopelia roseogrisea (S. risoria) (African collared dove)		
d (*d*, d^B, d^w)	Dark, blond (fawn), white	Z	Cole (1930)
ALB <H-R>	*S. tranquebarica humilis*-specific albumin	AL (linked to *hu-y*)	Miller and Weber (1969)
hu-8	*S. tranquebarica humilis*-specific erythrocyte alloantigen hu-8	AL (linked to *L*)	Miller (1964)
hu-y	*S. tranquebarica humilis*-specific erythrocyte alloantigen hu-y	AL (linked to *ALB*)	Miller and Weber (1969)
L	Silky	AL (linked to *hu-8*)	Miller (1964)
	Psittacula krameri (rose-ringed parakeet)		
cin	Cinnamon	Z	Rašek[8]
ino (*ino*, ino^{pd}, ino^{py})	Ino, pallid (lime), pearly	Z	Onsman[6]; Rašek8
op	Opaline	Z	Rašek[8]
bl (*bl*, bl^{tq}, bl^{aq})	Blue, turquoise(parblue), aqua(parblue)	AL (linked to *D*)	Rašek[8]
D	Dark	AL (linked to *bl*)	Rašek[8]

(continued)

Table 12 (Continued)

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
	Melopsittacus undulates (budgerigar)		
ACO1 <IREBP>	Aconitase 1, soluble	Z	Saitoh et al. (1993)
cin	Cinnamon	Z (closely linked to *ino* and *sl*)	Mason[5]; Onsman[6]
EMB <ZOV3>	Embigin homolog (mouse)	Z	Saitoh et al. (1993)
ino (*ino^{cb}*, *ino^{l}*, *ino^{pl}*, *ino*)	Clearbody, lime, platinum, lutino (sex-linked imperfect albinism)	Z (closely linked to *cin* and *sl*)	Mason[5]; Onsman[6]
op	Opaline	Z	Mason[5]; Onsman[6]
sl	Slate	Z (closely linked to *cin* and *ino*)	Mason[5]; Onsman[6]
bl (*bl^{1}*, *bl^{2}*, *bl^{tq}*, *bl^{gf}*; or *bl^{1}*, *bl^{2}*, *bl^{yf2}*, *bl^{gf}*) <*s, b*>[9]	Blue (blue 1, blue 2, turquoise, blue goldenface, blue yellowface 2)	AL (linked to *D*)	Onsman[6]; Hesford[10]
D	Dark	AL (linked to *bl*)	Mason[5]; Olszewski[11]
ACO1 <IREBP>	*Struthio camelus* (*ostrich*) Aconitase 1, soluble	Z	Ogawa et al. (1998); Tsuda et al. (2007)
ATP5A1	ATP synthase, H+ transporting, mitochondrial F1 complex, alpha subunit 1, cardiac muscle	Z, W	Tsuda et al. (2007)
CHD1	Chromodomain helicase DNA-binding protein 1	Z, W	Tsuda et al. (2007)
EMB <ZOV3>	Embigin homolog (mouse)	Z, W	Ogawa et al. (1998)
GHR	Growth hormone receptor	Z, W	Tsuda et al. (2007)
HINT1	Histidine triad nucleotide-binding protein 1	Z	Tsuda et al. (2007)
NTRK2	Neurotrophic tyrosine kinase, receptor, type 2	Z, W	Tsuda et al. (2007)
RPS6	Ribosomal protein S6	Z, W	Tsuda et al. (2007)
SPIN1	Spindlin 1	Z, W	Tsuda et al. (2007)
TMOD1	Tropomodulin 1	Z, W	Tsuda et al. (2007)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	O'Neill et al. (2000); Tsuda et al. (2007)
	Dromaius novaehollandiae (emu)		
ACO1 <IREBP>	Aconitase 1, soluble	Z, W	Ogawa et al. (1998)
DMRT1	Doublesex and mab-3-related transcription factor 1	Z	Shetty et al. (2002)
EMB <ZOV3>	Embigin homolog (mouse)	Z, W	Ogawa et al. (1998)
WPKCI-8 <Wpkci, HINTW, Wpkci-7, ASW>	W chromosome-specific histidine triad nucleotide-binding protein 1	W	O'Neill et al. (2000)

(continued)

Table 12 (Continued)

Loci linked (locus alleles) <aliases>	Trait name (synonym)	Chromosome (Z, W, 1) or autosomal linkage (AL)	Reference
	Casuarius casuarius (southern cassowary)		
ACO1 <IREBP>	Aconitase 1, soluble	Z	Nishida-Umehara et al. (1999)
EMB <ZOV3>	Embigin homolog (mouse)	Z, W	Nishida-Umehara et al. (1999)

[1] This locus appears to be the same as *g*

[2] Some authors (e.g., Lancaster, 1977) consider this gene to be autosomal

[3] Sokolovskaya (1935) and Hollander (1970) showed a homology between the loci ch in the Muscovy duck and d in the domestic duck

[4] Legg B. http://www.leggspeafowl.com/peafowlcolors.htm

[5] Mason AD. http://www.cabinsoftware.biz/Genetics_Tutorial/Part1.htm

[6] Onsman I. http://www.euronet.nl/users/hnl/; http://www.euronet.nl/users/dwjgh/

[7] Huntley RR. http://www.angelfire.com/ga/huntleyloft/

[8] Rašek M. http://www.gencalc.com/

[9] A universal nomenclature is required for this locus

[10] Hesford C. http://ourworld.compuserve.com/homepages/clivehesford/parblu04.html

[11] Olszewski A. http://www.petcraft.com/docs/avgen.shtml

Over the last decade, molecular tools and genetic maps have been developed in other avian species, and comparative avian genome studies have been boosted by creating the chicken genomic resources. From the field of comparative cytogenetics including ZOO-FISH studies, comparative mapping of BAC clones, and comparative chromosome G-banding, it is known that chicken chromosome 2 has split into chromosomes 3 and 6 of turkey and pheasants, while chicken chromosome 4 is a fusion between chromosome 4 and a microchromosome in many other birds (Shetty et al. 1999; Schmid et al. 2000, 2005; Raudsepp et al. 2002; Guttenbach et al. 2003; Derjusheva et al. 2004; Itoh and Arnold 2005). In the guinea fowl, chromosome 4 is the result of a centric fusion of chicken chromosome 9 with the q arm of chicken chromosome 4 (Shibusawa et al. 2002). Guinea fowl chromosome 5 represents the fusion of chicken chromosomes 6 and 7. A pericentric inversion in guinea fowl chromosome 7 corresponds to chicken chromosome 8. Chicken chromosome-specific paints from macrochromosomes 1–9 and Z hybridized to metaphases of the Japanese quail and red-legged partridge revealed no interchromosomal rearrangements (Schmid et al. 2000; Shibusawa et al. 2002; Kasai et al. 2003). Comparative FISH mapping of selected chicken BAC clones specific for macrochromosomes (GGA1–8, GGAZ) suggested strong conservation between sequences of the chicken, quail, turkey, and duck (Schmid et al. 2005) that represent two early evolutionary avian lineages split nearly 90 MYA. Several intrachromosomal rearrangements, fusions, or fissions were detected in four species. Evolution of karyotypes in birds seems to have proceeded slower in time than in mammals, which have more radical karyotype rearrangements. Avian karyotypes could have evolved via many fusion/fission and/or inversions instead of reciprocal translocations (Burt et al. 1999; Burt 2002; Schmid et al. 2005).

Comparative investigations also contributed to chicken genome mapping and cross-species application of molecular tools in chicken, turkey, guinea fowl, Japanese quail, duck, and pigeon (Pimentel-Smith et al. 2000; Smith et al. 2000a, 2001b; Reed et al. 2003; Schmid et al. 2005). Using FISH mapping and direct sequencing of genomic regions, several loci have been assigned to the sex chromosomes and autosomes in the turkey, peafowl, pheasants, quails, ducks, pigeon, ostrich, emu, cassowary, budgerigar, zebra finch (Table 12), and some other birds.

Comparative mapping using BAC contigs can provide a critical component of the genomic research in other birds. Large-insert BAC libraries are also available for several other avian species (Table 11). For instance, a zebra finch BAC library (Clayton 2004) with ~16-fold coverage was made at the Arizona

Genome Institute, an emu BAC library (13.5×) at the US Department of Energy Joint Genome Institute (Kellner et al. 2005), and a California condor (*Gymnogyps californianus*, family *Cathartidae*, order *Ciconiiformes*) BAC library with ~14-fold coverage by CHORI (Nefedov et al. 2003; Romanov et al. 2006). Genomic cosmid libraries have been constructed for the Japanese quail, pigeon, goose, emu and two passerines, red-winged blackbird (*Agelaius phoeniceus*) and brown-headed cowbird (*Molothrus ater*) (Kameda and Goodridge 1991; Edwards et al. 1998; Longmire et al. 1999; Shiina et al. 1999; Roots and Baker 2002; Takahashi et al. 2003), and a fosmid library for the domestic duck (Moon and Magor 2004). Large-insert contig physical maps of other avian genomes, aligned with the chicken sequence, would be valuable resources. Furthermore, these comparative maps would aid in the analysis and application of the chicken whole-genome sequence.

Thomas et al. (2002) demonstrated that so-called universal OVERGO probes, or Uprobes, can be used to identify orthologous BACs in a variety of mammals (primates, cat, dog, cow, pig) and, more recently, between vertebrate orders (Kellner et al. 2005). OVERGOs are designed from regions of high sequence conservation and then used to probe unsequenced genomes. Romanov and Dodgson (2006) analyzed cross-species hybridizations using OVERGOs that were derived from chicken genomic and zebra finch EST sequences and probed to turkey and zebra finch BAC libraries. OVERGOs within coding sequences were more effective than those within untranslated region (UTR), intron or flanking sequences. In general, interspecies hybridization was more successful between chicken and turkey than for more distant evolutionary comparisons (chicken-zebra finch or zebra finch-turkey). This strategy can be used to align BAC contig maps of other avians along the chicken genome sequence and to construct interspecific comparative maps.

Molecular markers and tools have been generated for the Japanese quail (e.g., Pang et al. 1999; Kayang et al. 2002), duck and goose (Maak et al. 2003; Huang et al. 2005, 2006b), pheasant (Baratti et al. 2001), peafowl (Hanotte et al. 1991; Hale et al. 2004), pigeon (Traxler et al. 2000), ostrich (Tang et al. 2003), emu (Taylor et al. 1999), budgerigar (Kamara et al. 2007), and other avian species. These tools should facilitate linkage map construction, which has lately become reality for the duck (Huang et al. 2006b). Its preliminary linkage map was developed by segregation analysis of microsatellite markers using an inbred Peking duck resource population that consisted of 12 full-sib families with a total of 224 F_2 individuals. As a result, 115 loci were placed into 19 linkage groups and 34 markers were unlinked. The total length of the preliminary sex-averaged linkage map for duck is 1,387.6 cM, as in other species. Integration of the genetic and cytogenetic map of the duck genome was done by FISH using chicken BAC clones, and 11 of 19 linkage groups were assigned to ten duck chromosomes (Huang et al. 2006b). The construction of a duck BAC library (Yuan et al. 2006) will pave the way for genome research in this poultry species.

A considerable breakthrough in genetic mapping of the Japanese quail genome has been achieved by designing molecular maps using AFLP and microsatellite markers. The first genetic linkage map contained 258 AFLP markers assigned to 39 autosomal linkage groups plus the Z and W sex chromosomes (Roussot et al. 2003). The first-generation microsatellite linkage map of this species included 58 markers resolved into 12 autosomal linkage groups and Z chromosome (Kayang et al. 2004). On the second-generation genetic linkage map, 1,660 AFLP and eight microsatellite markers, phenotype of a genetic disease (neurofilament-deficient mutant) and sex phenotype were assigned to 44 multipoint linkage groups, the W chromosome and 21 two-point linkage groups (Kikuchi et al. 2005). Six more microsatellite loci derived from ESTs (Mannen et al. 2005) and nine EST markers derived from cDNA-AFLP fragments (Sasazaki et al 2006a) were added to this map.

A subsequent contribution to the Japanese quail molecular linkage map and its enrichment with classical markers, such as plumage colors and blood proteins, was done by Miwa et al. (2005). These authors constructed maps for 14 autosomal linkage groups and the Z chromosome and the maps contained 69 microsatellite markers and five classical markers: yellow (*Y*), black at hatch (*Bh*), hemoglobin (*Hb-1*), transferrin (*Tf*), and prealbumin-1 (*Pa-1*). The study confirmed an earlier observation from FISH studies that the *Bh* locus was mapped on the long arm of chromosome 1 (CJA1) using the flanking sequence of *Bh* as a probe (Niwa et al. 2003). Miwa et al. (2006) mapped five other microsatellite markers and the panda (*s*) character to chromosome 4 (CJA4), suggesting the endothelin receptor B subtype 2 gene

(*EDNRB2*) as a candidate for the *s* locus that was confirmed in a follow-up study by Miwa et al. (2007).

Two microsatellite and the AFLP quail genetic maps were integrated and amended with the alignment of the quail linkage groups on the chicken genome sequence assembly and with interspecific FISH. Kayang et al. (2006) obtained a total of 14 autosomal and Z chromosome-specific linkage groups with 92 loci and aligned them with the AFLP map. The total map distance was 904.3 cM with an average spacing of 9.7 cM between loci. After aligning the quail linkage groups and the chicken sequence, marker order for nine macrochromosomes and 14 microchromosomes was found to be very similar between the two species. No interchromosomal rearrangements were detected for all 23 chromosomes, suggesting conservation of the aligned syntenic segments (Kayang et al. 2006).

In a separate effort, Sasazaki et al. (2006b) developed another integrated map for quail that comprised 1,995 markers, including 1,933 AFLP, three phenotypic loci (*Quv, LWC*, and sex) and 59 genes/ESTs, assigned to 66 linkage groups (including the W chromosome). The total linkage map length was 3,199 cM and an average marker interval of 5.0 cM. There were similar positions of the genes and their orders in the quail and chicken except within a known inversion on quail chromosome 2 (CJA2; Shibusawa et al. 2001). On the other hand, low map resolution did not allow detection of three other inversions previously found in CJA1, CJA4, and CJA8.

Another well-known laboratory bird is the zebra finch, referred to as "the mouse, or Drosophila of the avian world" (Arnold and Clayton 2004). Zebra finch is an Australian songbird that is a widely studied behavioral model, especially for mechanisms of learning and control of the male song, adult neurogenesis, and steroid synthesis in brain. There is a remarkable sexual dimorphism in brain regions controlling song. Interest in the genetic regulation of zebra finch behaviors has led to the generation of a BAC library, two EST projects, and a cDNA microarray (Arnold and Clayton 2004; Wade et al. 2004; Luo et al. 2006). Comparative cytogenetic analysis in the zebra finch using chicken chromosome paints suggested a very few chromosomal rearrangements since the evolutionary divergence of these two species, and a high conserved synteny of chicken genes and zebra finch orthologs (Itoh and Arnold 2005). Two major intrachromosomal rearrangements were detected that split chicken chromosome 1 into two macrochromosomes in zebra finches, and chicken chromosome 4 into a zebra finch macrochromosome and a microchromosome. Later on, zebra finch BAC end sequences and the whole BAC sequence were aligned with the chicken sequence, and a high degree of conserved synteny between two genomes was verified (Luo et al. 2006). BACs assigned by Romanov and Dodgson (2006) to zebra finch genes using cross-species hybridization are available online (US Poultry Genome Project, http://poultry.mph.msu.edu/resources/Resources.htm#bacdatafinch). The zebra finch will be the third avian species for which the BAC-contig physical map and sequence of the whole genome are available (Clayton et al. 2005).

A partial linkage map has been built for another passerine bird, great reed warbler (*Acrocephalus arundinaceus*; Hansson et al. 2005), as well as a comparative chicken-passerine microsatellite map (Dawson et al. 2006). The first linkage map for a passerine species included 43 microsatellite markers on 11 autosomal linkage groups and seven loci on the Z chromosome (Hansson et al. 2005). A predicted passerine map (Dawson et al. 2006) was based on the sequence similarity between 550 passerine microsatellites and the draft chicken genome sequence, and was also aligned with the Hansson et al. (2005) great reed warbler linkage map. A SNP-based Z chromosome map for 23 genes was created by Backström et al. (2006) using a natural population of collared flycatchers (*Ficedula albicollis*) and chicken genome sequence; conserved synteny with gene order rearrangements on the avian Z chromosome was demonstrated.

To initiate genomic studies for the California condor and take advantage of progress in chicken genomics, Raudsepp et al. (2002) attempted a broad cytogenetic analysis in this endangered species. As a result, a chromosome number of 80 was established (with a likelihood of an extra pair of microchromosomes), and information on the centromeres, telomeres, and nucleolar organizing regions was obtained. By hybridizing individual chicken chromosome-specific paints for 1–9 and Z and W on condor metaphase spreads, condor and chicken macrochromosomes were compared. Good correspondence of the chicken macrochromosomes with a single condor macrochromosome was observed, except for chromosomes 4 and Z. GGA4 was homologous to condor

chromosomes 4 and 9, supporting the idea that the latter are ancestral avian chromosomes. The GGAZ paint hybridized to both Z and W in the condor, suggesting incomplete differentiation of the condor sex chromosomes during evolution, contrary to data for sex chromosomes in all other nonratites studied (Raudsepp et al. 2002).

Additionally, a first-generation comparative chicken-condor physical map was developed using a condor BAC library and OVERGO hybridization approach (Romanov et al. 2006). The OVERGOs were designed using chicken (164 probes) and New World vulture (8 probes) sequences. After screening a 2.8 × subset of the total library, 236 BAC-gene assignments were identified, with an average success rate of 2.5 positive BAC clones per probe. A preliminary comparative chicken-condor BAC-based map contained 93 genes. Alignment of selected condor BAC sequences with orthologous chicken sequences showed a high conserved synteny between the two avian genomes. This study has created indispensable resources for seeking candidate loci for chondrodystrophy in condors and assisting genetic management of this disease (Romanov et al. 2006).

Currently, the active genome mapping and sequencing projects in birds include chicken, turkey, duck, Japanese quail, zebra finch, brown kiwi, and California condor (NCBI Entrez Genome Project database, http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=genomeprj). The majority of 1,075,888 nucleotides and 73,649 protein avian sequences deposited in GenBank (as of May 7, 2007) belong to chicken, turkey, zebra finch, duck, and condor; while chicken, pigeon, common and Japanese quail, and duck remain key avian models for biomedical research as assessed by the number of PubMed accessions (Table 13). Details on turkey genetics and genome mapping are given in Chapter 6 of this volume.

5.4 QTL and Functional Genomics

5.4.1 QTL Analysis

The identification of genes underlying the expression of economically important traits is a main research focus in agricultural genomics. Most of these traits are characterized by a wide variation in the expression of genes at certain loci called QTL (Cheng et al. 1995), which are polymorphic loci associated with variation in a phenotypic trait like egg production, body weight (BW), and so on. Characterization of the chromosomal regions carrying QTL can be applied in MAS to improve breeding efficiency (Grisart et al. 2002). Molecular linkage map, in combination with powerful statistical methods, facilitates the genetic dissection of complex traits, and the chicken is ideally suited for this task due to a relatively short life cycle and large number of progenies (Vallejo et al. 1998). Two major approaches are employed to understand genomic architecture underlying economically important traits: QTL mapping and, more recently, functional genomics.

QTL studies in chickens were started in the middle of 1990s using minisatellite markers and a technique known as genomic fingerprinting. In one of these studies, crosses of two genetically distinct lines of layer-type chickens and a single-trait animal model were used to identify genetic markers linked to QTL (Lamont et al. 1996). Analysis of associations of individual DNA fingerprint (DFP) bands of sires and their progeny phenotypic performance revealed QTL linked to specific traits of growth, reproduction, and egg quality QTL.

QTL have been identified for a variety of traits in chickens including growth (Groenen et al. 1997; van Kaam et al. 1998, 1999a; Tatsuda and Fujinaka 2001), feed efficiency (van Kaam et al. 1999a), carcass traits (van Kaam et al. 1999b), resistance to Marek's disease (MD; Vallejo et al. 1998; Xu and Goodridge 1998; Yonash et al. 1999; Lipkin et al. 2002), fatness (Ikeobi et al. 2002), and egg quality (Tuiskula-Haavisto et al. 2002; Wardecka et al. 2002), based on high-resolution genetic maps. Mapping information from QTL studies has enabled the further localization of 45 microsatellites on the consensus map resulting in a total number of 2,306 markers (Schmid et al. 2005).

5.4.2 QTL: Growth, Meat Quality, and Productivity

To elucidate QTL that affect growth, genome-wide scans with microsatellite markers has been employed. For example, van Kaam et al. (1999a) performed a whole-genome scan for QTL affecting growth and

Table 13 Number of accessions in the NCBI GenBank (Nucleotide and Protein) and PubMed databases for avian species with more than 300 deposited nuclear and mitochondrial nucleotide sequences[a]

Species/Order	Nucleotide/Protein	PubMed
Gallus gallus (chicken)/*Galliformes*	923,090/31,335	81,156
Taeniopygia guttata (zebra finch)/*Passeriformes*	67,726/263	275
Meleagris gallopavo (turkey)/*Galliformes*	18,052/411	299
Anas platyrhynchos (mallard)/*Anseriformes*	4,072/549	787
Gymnogyps californianus (California condor)/*Ciconiiformes*	970/4	8
Motacilla flava (yellow wagtail)/*Passeriformes*	890/91	4
Pygoscelis adeliae (Adelie penguin)/*Sphenisciformes*	671/17	55
Ficedula hypoleuca (European pied flycatcher)/*Passeriformes*	575/271	72
Ficedula albicollis (collared flycatcher)/*Passeriformes*	568/286	41
Coturnix japonica (Japanese quail)/*Galliformes*	538/425	4,093
Motacilla alba (white wagtail)/*Passeriformes*	498/259	5
Parus major (great tit)/*Passeriformes*	498/153	159
Luscinia svecica (bluethroat)/*Passeriformes*	422/200	10
Parus montanus (willow tit)/*Passeriformes*	416/168	18
Parus caeruleus (blue tit)/*Passeriformes*	411/84	74
Anas strepera (gadwall)/*Anseriformes*	409/47	9
Carpodacus erythrinus (common rosefinch)/*Passeriformes*	387/190	4
Columba livia (domestic pigeon)/*Columbiformes*	380/188	9,258
Strix aluco (tawny owl)/*Strigiformes*	328/175	42
Coturnix coturnix (common quail)/*Galliformes*	314/195	4,208
Dendrocopos major (great spotted woodpecker)/*Piciformes*	300/144	2

[a] As of May 7, 2007

feed efficiency in chickens and detected four QTL on GGA1, GGA2, GGA4, and GGA23 that exceeded the significance thresholds. The same research group has carried out a whole-genome scan in chicken for QTL affecting carcass traits (van Kaam et al. 1999b). Two QTL were shown to be located on GGA1 and GGA2. These results were confirmed and refined using Bayesian analysis (van Kaam et al. 2002).

Tatsuda and Fujinaka (2002) detected QTL affecting BW closely aligned with those reported using a reference population derived from a cross of a Satsumadori (slow-growing, light-weight Japanese native breed used as a meat chicken) sire and a White Plymouth Rock (early maturing, heavy weight broiler) dam. Two QTL affecting BW at 13 and 16 weeks were mapped at 220 cM on GGA1 and at 60 cM on GGA2. The closest QTL markers were *LEI0071* on GGA1 and *LMU0013* and *MCW0184* on GGA2.

QTL for BW at 3, 6, and 9 weeks of age were investigated by Sewalem et al. (2002) using a broiler × layer cross. A QTL on GGA13 influenced BW at all three ages and QTL significant at the genome-wide level that affected BW at two ages were found on chromosomes 1, 2, 4, 7, and 8.

Identification of QTL for meat quality and production in a commercial population of broilers was done by de Koning et al. (2004). Using genotypes for 52 microsatellite loci spanning regions of nine chicken chromosomes and a half-sib analyses with a multiple QTL model, linkage between these nine regions and growth, carcass and feed intake traits was established.

QTL affecting fatness in the chicken were investigated and mapped by Ikeobi et al. (2002) in an F_2 population developed by crossing a broiler line with a layer line. Using within-family regression analyses

of 102 microsatellite loci in 27 linkage groups, the QTL for abdominal fat weight were identified on chromosomes 3, 7, 15, and 28; abdominal fat weight adjusted for carcass weight on chromosomes 1, 5, 7, and 28; skin and subcutaneous fat on chromosomes 3, 7, and 13; skin fat weight adjusted for carcass weight on chromosomes 3 and 28; and skin fat weight adjusted for abdominal fat weight on chromosomes 5, 7. and 15. Significant positive and negative QTL alleles were detected in both lines. Several QTL affecting fatness in broilers were detected by Jennen et al. (2004) using two genetically different outcross broiler dam lines, originating from the White Plymouth Rock breed.

Genetic architecture of growth and body composition was investigated in reference chicken populations obtained by crossing one modern broiler male from a commercial broiler breeder male line with females from two unrelated highly inbred lines (Deeb and Lamont 2003). Traditionally selected phenotypic traits in broilers were suggested to be controlled by a large number of genes with small epistatic effects, while fitness-related traits could be determined by a lower number of genes with major effects.

After simultaneous mapping epistatic QTL in a chicken F_2 intercross, clusters of QTL pairs with similar genetic effects on growth were found by Carlborg et al. (2004). The authors used simultaneous mapping of interacting QTL pairs to study growth traits. This approach improved the number of detected QTL by 30%. The genetic variance of growth was significantly influenced by epistasis, the largest impact being on early growth (before 6 weeks of age). Because early growth was shown to be associated with a discrete set of interacting loci involved in early growth, these results provided further insight into different genetic regulations in early and late growth in chicken found in other studies.

5.4.3 QTL: Egg Quality and Productivity

Genome-wide scans for egg quality and productivity QTL have been done using reference populations, while a line cross between two egg layer lines was used in the study by Tuiskula-Haavisto et al. (2002). The authors determined 14 genome-wide significant and six suggestive QTL located on chromosomes 2, 3, 4, 5, 8, and Z. The most interesting area was found on GGA4, with QTL for BW, egg weight, and feed intake. A related investigation was done by Wardecka et al. (2002) to determine influence of genotypes of the Rhode Island Red (RIR) and Green-legged Partrigenous (GLP) breeds on egg production and quality traits based on analysis of 23 microsatellite markers. Significant effects were demonstrated for 16 traits.

Marker loci detected by QTL mapping can serve as multiple entry points into the physical BAC-contig map and sequence of the chicken genome. For example, two QTL from the aforementioned study were selected for FISH mapping using microsatellite-specific large-insert clones (Sazanov et al. 2005). This strategy helps to specify genes that might underlie QTL and is known as QTL positional cloning.

Genetic mapping of QTL affecting egg characters, egg production, and BW in F_2 White Leghorn (WL) × RIR intercross chickens was done by Sasaki et al. (2004) using 123 microsatellite markers. The authors assigned 96 markers to 25 autosomal linkage groups and 13 markers to the Z chromosome, including eight previously unmapped markers. Significant QTL were discovered for BW on chromosomes 4 and 27, egg weight on GGA4, the short length of egg on GGA4, and redness of egg shell color on GGA11. A significant QTL on GGAZ was found for age at first egg. Overall, 6–19% of the phenotypic variance in the F_2 population may be explained by these QTL.

5.4.4 QTL: Disease Resistance

Immune response and disease resistance can be improved by selection. Because these quantitative traits have low to moderate heritability, they may respond more efficiently to marker-assisted selection than to conventional selection (Yonash et al. 2001).

As an alternative to vaccination control, increased genetic resistance to Marek's disease (MD) represents an attractive solution for lowering disease outbreaks. Genetic mapping of QTL affecting susceptibility to MD virus-induced tumors was performed by Vallejo et al. (1998) and was the first to report the mapping of non-major histocompatibility complex (MHC) QTL involved in MD susceptibility in chickens. Two significant and two suggestive MD QTL were detected on four chromosomal regions. These loci explained 11–23% of the phenotypic MD variation, or 32–68% of the genetic variance.

Another QTL for MD explaining 7.2% of the total disease variation was revealed on GGA4 by Xu et al. (1998) using a heterogeneous residual variance model, which is considered to be computationally much faster than the mixture model approach. These and other studies that used the same F_2 cross between two experimental lines (Bumstead 1998; Yonash et al. 1999; Liu et al. 2001, 2003a) identified QTL on chromosomes 1, 2, 4, 7, 8, 12, and 17 that affect MD resistance. QTL associated with MD resistance (defined as survival time following challenge) were tested in a cross between lines of commercial layer chickens (McElroy et al. 2005). In this study, genotyping was performed using 81 microsatellites selected based on prior results with selective DNA pooling, and several markers associated with MD survival were identified. One of these markers corresponds to a QTL identified on GGA2 near the region identified for MD susceptibility by Vallejo et al. (1998) and Yonash et al. (1999), which is around 90 cM on the consensus map.

A very important issue for poultry production and food safety is the contamination with *Salmonella enteritidis* (SE). Kaiser et al. (2002) identified genetic markers of antibody (Ab) response to SE vaccine in broiler chicks and confirmed this linkage in broiler-cross offspring. Interactions of microsatellite marker alleles with dam line and sex were also detected.

Several QTL for immune response to sheep red blood cells (SRBC) were detected by Siwek et al. (2003a) in laying hens using 170 microsatellite markers, and F_2 resource populations originated from a cross of two divergently selected lines for high and low primary Ab response to SRBC. A half-sib model and a line-cross model, both based on the regression interval method, were used to identify QTL. The QTL involved in the primary Ab response to keyhole lympet hemocyanin and *Mycobacterium butyricum* were detected in two independent populations of laying hens (Siwek et al. 2003b). The genetic regulation of Ab responses to two different T- cell dependent antigens was suggested to differ.

QTL affecting the immune response were investigated using a linkage disequilibrium approach with microsatellites in hybrids of highly inbred males of two MHC-congenic Fayoumi chicken lines and highly inbred G-B1 Leghorn hens (Zhou et al. 2003). The QTL that affect Ab kinetics were localized on chromosomes 3, 5, 6, and Z.

A genome wide scan using 119 microsatellite loci allowed Zhu et al. (2003) to map QTL associated with disease resistance to avian coccidiosis to GGA1.

QTL associated with immune response to SRBC, Newcastle disease virus, and *E. coli* and with survival were investigated by Yonash et al. (2001). Three markers were shown to have significant association with these traits.

Besides its own economic importance, the chicken can be considered as a model object for human diseases, e.g., for genetic susceptibility to form-deprivation myopia (Guggenheim et al. 2002; Dodgson and Romanov 2004; Jensen 2005).

5.4.5 QTL: Behavior

Several QTL affecting feather pecking (FP) behavior (which is a major problem in large group housing systems) and stress response in laying hens were detected by Buitenhuis et al. (2003) Using genotypes at 180 microsatellite loci, one significant QTL for severe FP was detected on GGA2, and suggestive QTL for gentle FP on GGA1, GGA2, and GGA10.

A genome-wide scan using 104 microsatellite markers was performed to identify QTL affecting foraging behavior and social motivation QTL in F_2 progeny from a WL × red junglefowl intercross (Schutz et al. 2002). Significant QTL were found for preference of free food without social stimuli and low contra-freeloading on GGA27 and GGA7, respectively. Interestingly, the location of the QTL coincided with known QTL for growth rate and BW.

QTL studies in the chicken have rapidly expanded, and a specialized chicken QTL database has been created (NAGRP, http://www.animalgenome.org/QTLdb/chicken.html). With the availability of dense genetic linkage maps, QTL studies are becoming more feasible in other poultry species (e.g., Minvielle et al. 2005; Beaumont et al. 2005; Huang et al. 2007).

5.4.6 Toward Functional Genomics of Poultry

The chicken has been an attractive model organism in the field of fundamental biology and medicine for at least 100 years, for instance with the discovery of B

cells and tumor viruses (Brown et al. 2003; Romanov et al. 2004). The avian embryo is an ideal system for studies of vertebrate development (e.g., limb bud) because of the ease of access and manipulation using incubated eggs (Stern 2004, 2005). Avian functional genomics is a new promising research area due to increased genetic resources and tools including EST programs, DNA microarrays, electroporation of chicken embryos, use of RNAi to knock down gene expression, and transgenic technologies (Brown et al. 2003; Stern 2004; Burt 2005).

DNA microarrays have become a powerful tool for determining functional genes in several organisms including human, rodents, fruit fly, chicken, etc. An international, US-French consortium for systems-wide chicken gene expression profiling was established in 2000 (Cogburn et al. 2003). The goal of the project was to provide genomic resources (ESTs and DNA microarrays), examine global gene expression in target tissues of chickens, and facilitate discovery of functional genes. Another chicken functional genomics initiative led by the UK consortium resulted in the collection of 339,314 ESTs from 64 cDNA libraries derived from 21 tissues of adult hens and chicken embryos (Boardman et al. 2002). These DNA sequences were organized in 85,486 contigs corresponding to 89% of estimated total number of chicken genes. Around 180,000 of these ESTs represented novel coding sequences in the chicken, while 38% of them were orthologous to sequences in other species. Later on, the merging of the UK (300,000) and US (30,000) EST collections took place (reviewed by Romanov et al. 2004). Currently, there are 599,330 ESTs deposited in the NCBI dbEST database (as of May 7, 2007).

Affymetrix, Inc. has developed the first commercially available GeneChip Chicken Genome Array (Affymetrix, http://www.affymetrix.com/products/arrays/specific/chicken.affx). This array includes 25-mer oligonucleotide probes for identifying 32,773 transcripts corresponding to over 28,000 chicken genes, as well as 689 probe sets for 684 transcripts from 17 avian viruses. Other chicken whole-genome long oligo arrays include: (1) the Operon Biotechnologies, Inc. 70-mer array with 21,120 features designed by ARK-Genomics (Roslin, UK) and manufactured by the University of Arizona Genomics Research Lab (GRL, Tucson, AZ, USA); (2) the Chicken Consortium cDNA array with 11,136 × 2 features also produced by GRL; and (3) the NimbleGen Systems, Inc. Chicken ChIP- chip that tiles every 100 bp across nonrepetitive regions. A new 44,000-element long oligonucleotide chicken array was also made by Agilent Corp. A collaborative team from the Roslin Institute (Edinburgh, UK), University of Delaware (Newark, DE, USA), GSF Institute of Molecular Radiation Biology (Neuherberg, Germany) and the Fred Hutchinson Cancer Research Center (Seattle, WA, USA) produced a publicly available microarray containing ~13,000 chicken ESTs (Burnside et al. 2005). Additional chicken microarrays include four University of Delaware custom arrays (UD_Liver_3.2K, UD 7.4K Metabolic/Somatic Systems, Chicken Neuroendocrine System 5K, and the DEL- MAR 14K Integrated Systems), three ARK-Genomics arrays (an 1153 clone chicken embryo array, a 5,000 cDNA chicken immune array, and a 4,800 clone chicken neuroendocrine array) (US Poultry Genome Project, http://poultry.mph.msu.edu/about/Poultry%20Coord%20report%20for%2006.pdf; Smith et al. 2006).

These and other chicken microarray resources have been used for analyzing gene expression profiles in connection with immune responses to infectious diseases (e.g., Bliss et al. 2005; Smith et al. 2006; van Hemert et al. 2007), growth traits, lipid metabolism and fatness (Cogburn et al. 2003; Bourneuf et al. 2006; Wang et al. 2006), differentially expressed transcripts in shell glands (Yang et al. 2006), and embryonic development (Afrakhte and Schultheiss 2004; Ellestad et al. 2006) in experimental and commercial strains.

5.5 Other Molecular Applications

5.5.1 Biodiversity Studies

Genetic resources refer to races or populations with unique genetic characteristics. Agricultural resources need to be conserved for genetic adaptation to changes in agricultural production conditions and consumer preferences as well as for preservation of native (sometimes called local or "heritage") breeds. Thus, genetic resources in agricultural production systems require further identification, evaluation, and proper utilization for the welfare of humanity

and nature. Although often underestimated, the need to conserve and utilize genetic resources as a safeguard against an unpredictable future is evident (FAO 1997–2004; El Bassam 1998; Romanov and Weigend 2001a, b).

There is a growing loss of genetic diversity in all agriculturally used species, and poultry genetic resources are one of the most vulnerable (Scherf 2000; Weigend and Romanov 2001, 2002). The current market-oriented breeding strategies in poultry concentrate on a few specialized breeds that may cause a significant erosion of local breeds, leading to the loss of valuable genetic variability and unique characteristics of these breeds (Weigend et al. 1995). For instance, few decades ago there were more than 50 chicken breeds in North America, while only two for meat production are left, the others being mainly lost (Scherf 2000).

On the whole, in the world poultry market a limited number of breeding companies dominate and use a similar gene pool. The economic importance of single-purpose high-performance breeds is distorting the perception of the value of multipurpose breeds that are adapted to local conditions, from the point of view of the broader gene pool. According to Sørensen (1997), there is concern by the general public and the poultry industry that "cage-adapted populations of laying hens seem to have lost some of their abilities when returned to the old floor/free range systems." Due to a growing concentration of all components of the poultry production, less than ten world's breeding companies are the source of most egg laying hens. Until recently, these companies have little interest in improving genetic material for the West-European region, with noticeable consumer preferences for eggs produced in noncaged systems (Sørensen 1997). This situation could get worse under global epidemic challenges like avian influenza.

On the other hand, genetic studies (e.g., Dunnington et al. 1994; International Chicken Polymorphism Map Consortium 2004) showed that the pure lines of broiler and layer stocks in USA and other world regions still contain a considerable reservoir of genetic variation as estimated by DNA fingerprint (DFP) analysis and other molecular tools.

The evaluation of genetic diversity within and between both native and commercial chicken populations has been undertaken so far using the following molecular markers and techniques:

- RFLP (e.g., Wakana et al. 1986; Akishinonomiya et al. 1994; Wang et al. 1994),
- DFP (e.g., Dawe et al. 1988; Siegel et al. 1992; Haberfeld et al. 1992; Wimmers et al. 1992; Dunnington et al. 1994; Yamashita et al. 1994; Plotsky et al. 1995; Meng et al. 1996; Semyenova et al. 1996),
- RAPD (e.g., Plotsky et al. 1995; Romanov and Weigend 2001a),
- AFLP (e.g., Lee et al. 2000),
- microsatellites (e.g., Romanov and Weigend 2001b; Hillel et al. 2003),
- sequencing and SNP (e.g., Akishinonomiya et al. 1994; Schmid et al. 2005).

Multiple applications of molecular markers for biodiversity studies in poultry, mostly, in chickens, have been reviewed and listed elsewhere (e.g., Weigend and Romanov 2001, 2002; Soller et al. 2006; Michigan State University, http://www.msu.edu/ ~romanoff/biodiversity/studiesdb.htm).

5.5.2 Molecular Sexing

Sex identification methods in domestic and wild birds have been developed to distinguish between males and females, when no or weak sexual dimorphism is evident either at hatch, maturity, or in ovo. The usefulness of DNA sex determination has been demonstrated for evolutionary studies, ecological and conservation problems, and management of endangered species in the wild and captivity (e.g., Millar et al. 1996; Ellegren and Fridolfsson 1997; Kahn and Quinn 1999; Bermudez-Humaran et al. 2002).

Traditionally, sex linkage of external traits (autosexing; e.g., Spillman 1908; Staško 1970; Lancaster 1977; Romanov and Bondarenko 1988), vent sexing, surgical gonad examination and later, analyses of karyotype and the amount of DNA per cell (e.g., Wang and Shoffner 1974; Nakamura et al. 1990) have been applied for this purpose. With the advance of sophisticated molecular tools, it is now possible to obtain gender-specific DNA fingerprints. Because in birds the homogametic sex is the male with two Z chromosomes, and the heterogametic sex is the female with one Z and one W chromosomes, the molecular sexing techniques in avian species are principally based

on targeting the repetitive (e.g., Kagami et al. 1990; D'Costa and Petitte 1998; Cassar et al. 1998; Trefil et al. 1999), nonrepetitive (Ogawa et al. 1997), or coding regions in the W chromosome that are absent or different from their homologs in the Z chromosome.

PCR-amplified molecular markers make it possible to discriminate bird sexes based on Z- and W-chromosome-specific homologous sequences. Most known avian sexing markers are derivatives of two conserved gene homologs, *CHD1Z* and *CHD1W*, which encodes chromodomain helicase DNA-binding protein 1 that plays an important role in gene regulation (Ellegren 1996; Griffiths et al. 1996, 1998; Griffiths and Korn 1997; Kahn et al. 1998; Fridolfsson and Ellegren 1999).

5.6 Conclusions

In conclusion, contemporary avian genetics addresses biological questions at the genome-wide level. In the course of the last century, an enormous wealth of information has been accumulated regarding genetics, physiology, and biochemistry of poultry species. The chicken exemplifies both an important agricultural species and a model organism for studying the evolution of vertebrate genomes and developmental mechanisms. The success of the chicken genome project has been preceded by decades of genetic linkage mapping.

As a prominent experimental model in the last century for various fundamental and applied biologic disciplines, the chicken will keep its significance in the twenty-first century. The chicken genome sequence annotated with gene functions will pave the way for improving traits of economic importance and value in poultry (Romanov et al. 2004). The recent draft of the chicken genome sequence can also be used as a reference in comparative mapping, making up for the lack of knowledge in genetics and genomics of other domestic and wild birds and addressing global questions in biology of avian and vertebrate genomes.

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