Crossing Over in Chicken Oogenesis: Cytological and Chiasma-Based Genetic Maps of the Chicken Lampbrush Chromosome 1

A. V. Rodionov, N. A. Lukina, S. A. Galkina, I. Solovei, and S. Saccone

Chiasmata in diplotene bivalents are located at the points of physical exchange (crossing-over) between homologous chromosomes. We have studied chiasma distribution within chicken lampbrush chromosome 1 to estimate the crossing-over frequency between chromosome landmarks. The position of the centromere and chromosome region 1q3.3–1q3.6 on lampbrush chromosome 1 were determined by comparative physical mapping of the TTAGGG repeats in the chicken mitotic and lampbrush chromosomes. The comparison of the chiasma (=crossing over)-based genetic distances on chicken chromosome 1 with the genetic linkage map obtained in genetic experiments showed that current genetic distances estimated by the high-resolution genetic mapping of the East Lansing, Compton, and Wageningen chicken reference populations are 1.2–1.9 times longer than those based on chiasma counts. Conceivable reasons for this discrepancy are discussed.

Lampbrush chromosomes (LBCs) are giant diplotene bivalents that appear in the growing intrafollicular oocytes of chickens after 2–3 weeks of posthatching development (Gaginskaya and Chin 1980). They provide an excellent system for the study of chromosome polymorphism in birds and for gene mapping (Chelysheva et al. 1990; Hutchison 1987; Mizuno and Macgregor 1998; Rodionov et al. 1989; Solovei et al. 1993, 1998). Each chicken lampbrush bivalent possesses one or few chiasmata. Because chiasmata in diplotene bivalents are a reliable indicator of reciprocal recombination events (crossing over) (Carpenter 1994; Tease and Jones 1995), we earlier used them to estimate the crossing over frequency in chicken oogenesis and to identify the hotspots of recombination in the chicken macro- and microchromosomes (Rodionov et al. 1992a,b). In the present work we studied the chiasma distribution along chicken chromosome 1 to estimate the crossover-determined genetic linkage between chromosome markers. The chiasma (=crossing over)-based genetic length of the 1p and 1q arms and the corresponding distances measured in molecular genotyping experiments (Groenen et al. 2000; http://www.ri.bbsrc.ac.uk/chickmap/; http://poultry.mph.msu.edu/; http://www.zod.wau.nl/vf/hickensite/chicken.html) were compared.

Materials and Methods

Mitotic chromosome preparations were made from chicken embryos. At the fourth day of incubation, 0.2 ml of 10 μg/ml Colcemid (Gibco, Paisley, UK) was injected into each egg on the air-cell membrane. After a 2 h exposure, the embryo was removed from the egg and suspended by gently stirring with a Pasteur's pipette in a hypotonic mix of 1.25% sodium citrate and 1.0% KCl (1:1). The cell suspension was left at 37°C for 20–30 min and then centrifuged at 200g for 10 min. After three changes of methanol/acetic acid fixative (3:1 v/v) at 4°C (30 min, overnight, and 10 min) the chromosome preparations were made by dropping 5–8 drops of suspension on cold slides and then flame or air drying.

The technique for working with the chicken LBCs was, in general, the same as described by Solovei et al. (1993). The staining of LBCs with Coomassie blue R250 (Merck, Darmstadt, Germany) and DAPI (Serva, Heidelberg, Germany) was carried out as described by Macgregor and Varley (1988). The chromosomes of 35 sexually mature chickens (commercial line) were analyzed. Identification of macrobivalents was carried out by using the cytological map of the chicken lampbrush chromosomes (Chelysheva et al. 1990). One hundred well-spread chicken LBC 1 were selected and photographed to study

From the Biological Institute, St. Petersburg State University, Stary Peterhof, St. Petersburg 198504, Russia (Rodionov, Lukina, and Galkina), Zoology Department, Leicester University, Leicester, England (Rodionov and Solovei), Institute fuer Anthropologie und Humangenetik, Ludwig Maximilian Universitaet, Muenchen, Germany (Solovei), and Dipartimento di Protezione e Valorizzazione Agroalimentare—Sez. Allevamenti Zootecnici, University of Bologna, via F.lli Rosselli, 107, Reggio Emilia, Italy (Saccone). Different parts of this work were supported by the Royal Society, INTAS (grant no. 97-1610), the Russian Basic Research Foundation (grant no. 00-04-49327). The authors thank Prof. E. R. Gaginskaya of the St. Petersburg University Microscopic Research Center "Chromas" (RBRF no. 00-04-55013) and the Ministry of Science and Technology Research Program "Comus-1" (no. 06-03) for technical support. We are grateful to Prof. Herbert Macgregor for his support of this research and for critical reading of the manuscript. Address correspondence to Alexander V. Rodionov at the address above or e-mail: Alexander.Rodionov@pobox.spbu.ru.

chiasma distribution within bivalents. The sites of the $(TTAGGG)_n$ in chicken chromosomes were detected using the plasmid pHuR 93 that contain 40 copies of the TTAGGG unit (Moyzis et al. 1988). It was labeled with biotin-16-dUTP by the nick-translation kit (both from Boehringer, Mannheim, Germany). The hybridization mixture contained 1.2 μg/ml probe DNA in 50% formamide, 2× SSC, 10% dextran sulfate, 100 μg/ml *Escherichia coli* tRNA, and 20 μg/ml GC-enriched *Micrococcus* carrier DNA (Sigma, St. Louis, MO) at pH 7.0. The fluorescence in situ hybridization (FISH) protocol followed that of Solovei et al. (1993). TTAGGG-positive hybrid signals were observed in 21 lampbrush bivalents 1 and 74 mitotic chromosomes 1. The percentage of bivalents and mitotic chromosomes exhibiting the signals was estimated for each site.

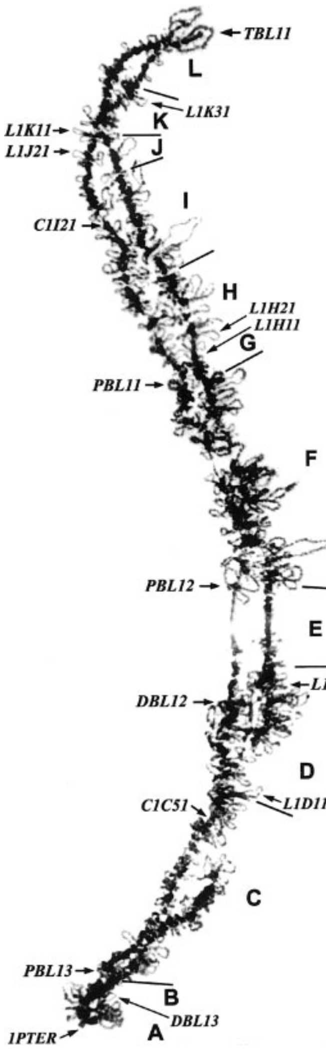

Figure 1. Chicken lampbrush chromosome 1 stained by Coomassie blue R250. The landmarks of chromosome regions A–L and some marker loops are shown. *1PTER,* telomere of the 1p arm; *TBL11,* telomeric bowlike loop on the 1q telomere; *PBLs,* the loops on the proximal border of loopless regions; *DBLs,* the distal border loops of the loopless regions; *L1D11, . . ., L1H21, . . ., L1K31,* marker loops; *C1C51* and *C1I21,* marker chromomeres. See also the legend of Figure 3.

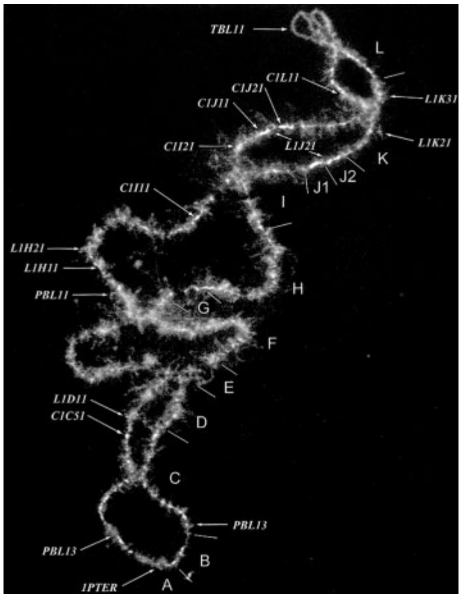

Figure 2. Chicken lampbrush chromosome 1 stained by DAPI. The A–L chromosome regions and some markers are shown. *1PTER,* the 1p arm telomere; *TBL11,* telomeric bowlike loops of the 1q telomere; *PBL13* and *PBL11,* proximal border loops of loopless regions; *L1D11, . . ., L1H21, . . ., L1K31,* marker loops; *C1C51, . . ., C1L11,* marker chromomeres. See also the legends of Figures 1 and 3.

Results and Discussion

Cytological Map of the Chicken Lampbrush Chromosome 1

LBC 1, the largest bivalent of the chicken chromosome set, is presented in the Figures 1–3. The figures demonstrate that chicken macrobivalent LBC 1 exhibits a distinct longitudinal differentiation, a specific loop-chromomere pattern. A working map of the chicken lampbrush macrochromosomes showing the lateral loop pattern was prepared by Chelysheva et al. (1990). It was constructed on the basis of 15–25 bivalents of each of the chicken macrochromosomes. In the present study, 100 well-spread chicken LBC 1 were selected and photographed. An analysis of these chromosomes allowed us to identify some new chromosome markers and to draw a new version of the chicken LBC 1 map (Figure 3). The map is patterned on the two main types of lampbrush chromosome markers, lateral loops with distinctive appearances and marker DAPI-positive chromomeres. On the map, they are designed by the letters *L* and *C,* respectively. The next character of the marker symbols shows the chromosome number, then a letter referring to the chromosome region name, and then a number of subregions. A final character in each LBC marker symbol is an individual number of either the loop or chromomere within the chromosome subregion; for example, *L1F21*—the first loop of subregion 2 of region F of LBC 1. For a few marker loops that were identified and designated earlier (Chelysheva et al. 1990) we used “traditional” names, for example, *TBL11* for the telomeric-bow-like loop of the 1q telomere; PBLs and DBLs for the proximal and distal border loops of the loopless bars (see Chelysheva et al. 1990; Solovei et al. 1994). Figures 1–3 show that LBC 1 is conveniently split into 12 regions (A–L) and a few subregions, each of them characterized by a modal length of lateral loops, few marker loops, and chromomeres.

Correspondence Between Chromosome Regions of the Chicken Lampbrush and Mitotic Chromosome 1

To determine the position of the centromere in the chicken LBC 1 the internal sites of the TTAGGG repeat were mapped in both lampbrush and mitotic chromosomes. Figure 4 shows TTAGGG probe hybridization in the chicken mitotic chromosomes. In 68 of all 74 (92%) mitotic chromosomes examined, the 1p telomere carries a TTAGGG-positive signal. The 1q telomere was labeled in 36.5% of cases. There were also distinct interstitial TTAGGG-positive sites (ITSs) in the regions 1p1.1, 1p2.6–1p2.8, and 1q3.3–1q3.5 (74%, 49%, and 63.5% of labeled chromosomes, respectively). The position of these ITS sites corresponds well with data published earlier by Nanda and Schmid (1994). In the regions 1p2.2–1p1.6 and 1q1.1 we observed a faint TTAGGG-positive signal on 2 of 74 (3.0%) studied chromosomes. The same pattern was observed in meiotic LBC 1 (Figure 5). TTAGGG-positive signals were found on the telomeres and in few nontelomeric sites (see also Solovei et al. 1994). A cluster of the interstitial $(TTAGGG)_n$ sequence, ITS11, was found in the region 1B. It was observed in 4 of 21 (19%) studied bivalents. Another one called ITS12 was localized on the border of subregions 1C1 and 1C2 [19 of 21 (90.5%) examined bivalents]. The third site, ITS13, was found in the 1C5 region (9.5% of labeled bivalents). Two ITS sites, ITS14 and ITS15, were found in the region 1E (86% and 9.5% of labeled bivalents, respectively). The last chromomere of the region 1J1 carries the signal in 19 (90.5%) of the LBC 1 studied. In a few preparations (2 of 21) there was also a weak

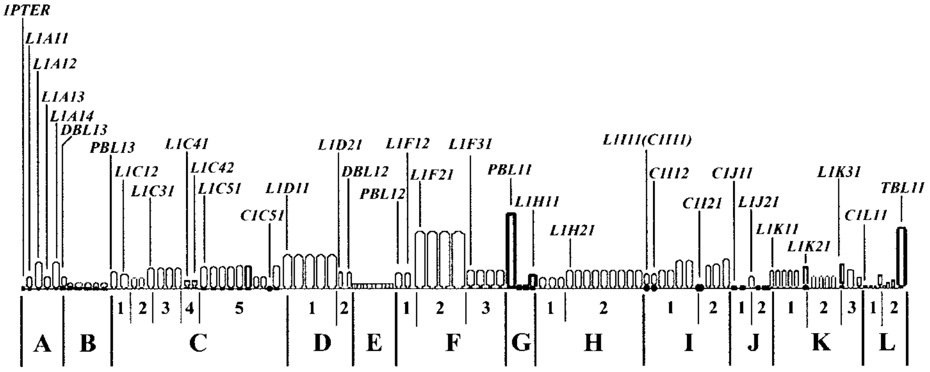

Figure 3. Cytological map of the chicken lampbrush chromosome 1. The map shows the landmarks of chromosome regions, some marker loops and chromomeres, and the modal length of the lateral loops in each region. Bold loops (*PBL11, L1H11, L1K21, L1K31,* and *TBL11*) correspond to the loops with matrix strongly stained by Coomassie blue R250. Separate brilliant chromomeres (*C1C51, C1I11, C1I21, C1J11*) are shown as black dots on the chromosome axis. A–L chromosome regions: *1PTER,* telomere of the 1p arm; *TBL11,* telomeric bowlike loop on the 1q telomere; *PBLs,* the loops on the proximal border of loopless regions; *DBLs*, the distal border loops of loopless regions; *L1A11, . . ., L1C31, . . ., L1K31,* marker loops; *C1C51, C1I11, . . ., C1L11,* marker chromomeres. Some loops (e.g. *L1A11, L1C12, L1C41, L1F31,* and some others) cannot be identified on the photographs of Figures 1 and 2.

TTAGGG-positive signal within region 1L1, ITS17. In general, the location of the distinct TTAGGG-positive telomeric and interstitial signals that were detected in the chicken LBC 1 coincides well with those in mitotic chromosomes (Figure 6). It may be suggested that the dissimilar percentage of mitotic and meiotic chromosomes with TTAGGG-positive FISH signals at some ITS sites is attributable to the different transcription activity of different TTAGGG clusters at the LBC stage (see Solovei et al. 1994).

From the data in Figure 6, it is clear that centromeric TTAGGG-positive signals of the chicken mitotic chromosome 1 correspond to those located within the region 1E. The loopless bar of region 1E appears to be the centromeric C-band of the chicken mitotic chromosome 1. The dark G-band cluster 1q3.2–1q3.6 appears to take the form of double DAPI-positive chromomere cluster 1J1 + 1J2 (Figures 2 and 3). The DNA sequences of either region 1K1 (L1K21) or region 1I2 (C1I21) are probably also included in the bands 1q3.2 or 1q3.6. Both ITS11 and ITS12 are located in the subterminal of the 1p arm. In a few cases, two separate TTAGGG-positive signals were resolvable either along or across chromatids of mitotic chromosomes in this region.

Chiasma-Based Genetic Linkage Between Chromosome Markers of Chicken Chromosome 1

The genetic distance between chromosome markers can be estimated on the basis of late recombination nodules (RNs) and chiasmata frequency (Morton et al. 1982; Peterson et al. 1999). There are many observations which indicate that the distribution of late RNs convincingly parallels that of crossovers (Croft and Jones 1989; Sherman and Stack 1995). Also there are extensive experimental and theoretical evidences that meiotic chiasmata in diplotene chromosomes correspond in position to the sites of genetic crossovers (Jones 1987; Tease and Jones 1995).

If chiasmata in diplotene bivalents are reliable indicators of reciprocal recombination events (crossing over), the crossover-determined genetic linkage between chromosomal markers *i* and *j* can be estimated on the basis of chiasma frequency within the *i-j* chromosome region as 50% of mean chiasma frequency, since one chiasma exhibits recombination in two of the four chromatids of a meiotic bivalent (Morton et al. 1982). Graphical representation of the chiasma (= crossover)-based genetic distance between chromosome markers of the chicken chromosome 1 is shown in Figure 6a. The chiasma-based genetic map of the chicken chromosome 1 spans 385 cM and consists of 27 chromosome markers. The chiasma-based map of LBC 1 exhibits characteristic features of eukaryotic genetic maps such as suppressed recombination in the pericentromeric region E and expansion of the genetic map in both subtelomeric regions.

Effects of Crossing Over and Other Recombination Mechanisms on the Genetic Map of Chicken Chromosome 1

In the chicken oocytes the mean RN frequency is 57.5 (range 51–69) (Rahn and Solari 1986). This number is close to the

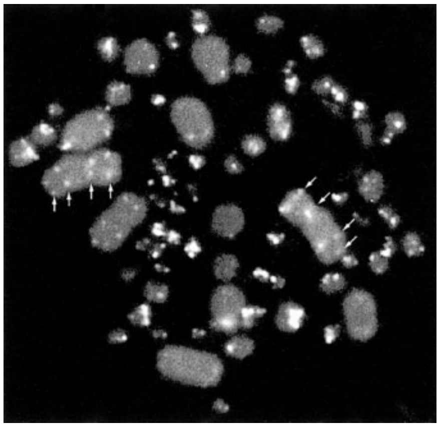

Figure 4. Propidium iodide-stained chicken mitotic chromosomes hybridized to the $(TTAGGG)_n$ sequence. The internal TTAGGG-positive sites (ITSs) of chromosome 1 are indicated by arrows.

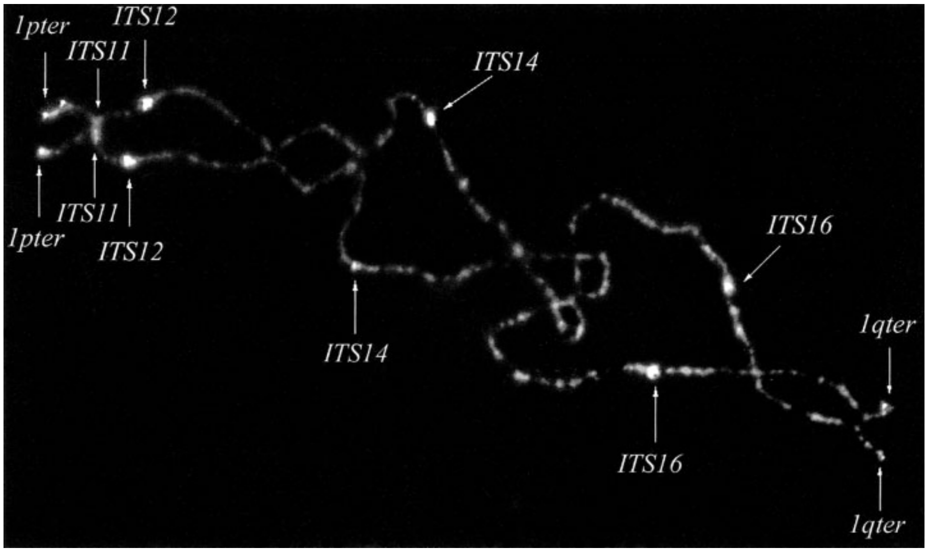

Figure 5. Propidium iodide-stained chicken lampbrush bivalent 1 hybridized to the $(TTAGGG)_n$ sequence. Hybridization signals were detected with FITC. Arrows show hybrid signals.

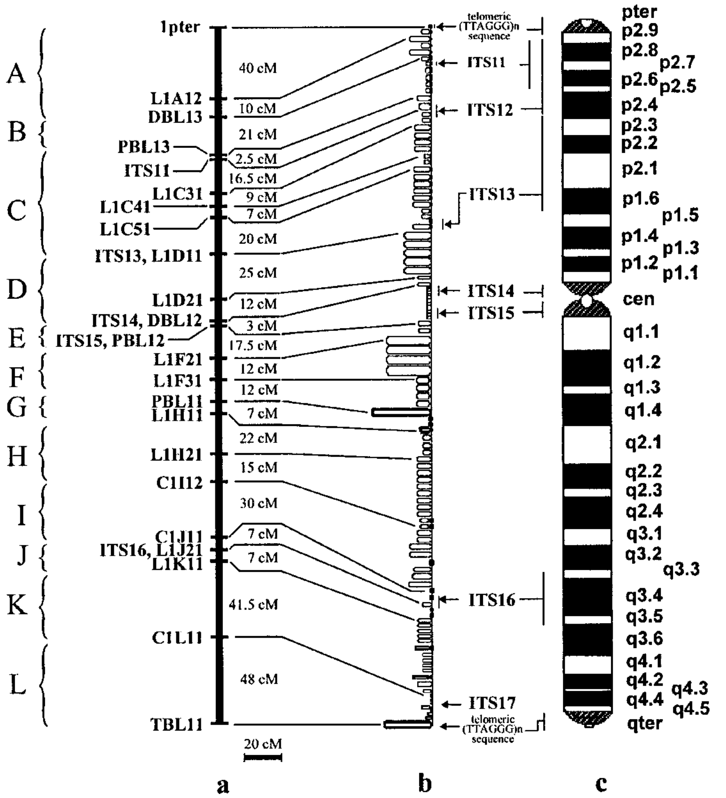

Figure 6. Chiasma-based genetic linkage between chromosome markers and correspondence between TTAGGG-positive signals on the chicken lampbrush and mitotic chromosome 1. (**a**) Chiasma-based genetic linkage between chromosome markers. (**b**) Cytological map of the chicken lampbrush chromosome 1 (for legend see Figure 3). (**c**) The ideogram of the banded chicken chromosome 1 according to Ladjali-Mohammedi et al. (1999) and http://www.ri.bbsrc.ac.uk/chickmap with small modifications. *ITS11–ITS17,* interstitial TTAGGG-positive loci of chromosome 1.

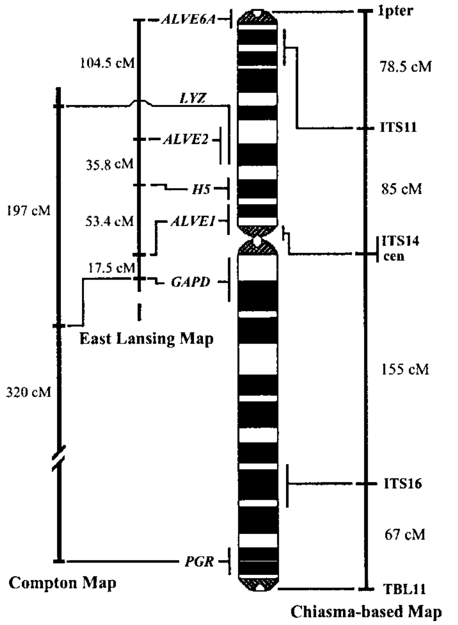

Figure 7. The comparison between genetic distances of the Compton and East Lansing genetic maps (http://www.ri.bbsrc.ac.uk/chickmap/; http://poultry.mph.msu.edu/) and the chiasma-based genetic map of the chicken chromosome 1.

number of chiasmata (about 59–64) per nucleus at the LBC stage (Rodionov et al. 1992b). The number of both RNs and chiasmata in bird oocytes (Pigozzi and Solari 1999; Rahn and Solari 1986; Rodionov et al. 1992b) and spermatocytes (Pigozzi and Solari 1999; Pollock and Fechheimer 1978) is nearly the same. It agrees with the equal length of the male and female chicken linkage maps estimated in genotypic studies (Groenen et al. 2000; http://www.ri.bbsrc.ac.uk/chickmap/; http://poultry.mph.msu.edu/). However, the total genetic length of the chicken genome (about 2800–3300 cM) estimated on the basis of chiasma frequency (Bitgood and Shoffner 1990; Rodionov et al. 1992b) is much less than the total length of the current chicken genetic maps (Groenen et al. 2000). The genetic distance between the terminal markers of the current genetic map of chromosome 1 estimated in molecular genotypic experiments (565 cM; see Smith et al. 2000) is much more than the chiasma-based genetic length (385 cM; our data), even though the markers cover only 94% of chromosome 1's physical length (Smith et al. 2000). The reason is probably that the genetic distance between loci *i* and *j* (W_{ij}), in addition to meiotic crossing over, is a function of additional recombination events such as mitotic crossing over and genetic conversion. In addition, nonparent types of gametes, which may be misperceived in genetic analysis as recombinant, are produced by premeiotic gene mutations in germ-line cells (Broman et al. 1998; Gorlov et al. 1993; Sybenga 1996). The misclassification of nonrecombinant alleles as double recombinants also effects the W_{ij} measured in molecular genetic experiments (Broman et al. 1998; Goldstein et al. 1997; Gorlov et al. 1993; Shields et al. 1991; Sybenga 1996). It was shown also that current computer programs, to account for the effect of interference based on the Kosambi's mapping function, especially MapMaker (Lander et al. 1987), produce map inflation when large numbers of markers are used in analysis (Sybenga 1996).

To make a rough estimate of the effect of noncrossover recombination mechanisms as well as computerized mapping inflation and errors of allele classification on the total genetic length of chicken chromosome 1, we compared the experimentally measured and chiasma-based genetic linkage between some physically mapped genes (Figure 7). Map distance $W_{1pter-1cen}$, the genetic length of the 1p arm measured in genetic experiments, can be calculated as approximately the length between subtelomeric locus *ALVE6A* that sets the physical and genetic boundary for the 1p terminus (Hutchison N, unpublished data, cited in Cheng et al. 1995; Smith et al. 2000) and the pericentromeric loci *ALVE1* and *GAPD* that are physically mapped in 1p1.2–p1.1 and 1q1.1–q1.2, respectively (Ponce de Leon et al. 1991; Hutchison N, unpublished data). Therefore it appears that $W_{1pter-1cen}$ is more than 193.68 cM (map distance between *ALVE6A* and *ALVE1*) but less than 211.16 cM (distance between *ALVE6A* and *GAPD*) of the East Lansing map. Thus the current genetic map of the chicken 1p arm is about 1.2–1.3 times more than the genetic length of the 1p arm determined by crossing over (163 cM versus 193–211 cM). In the case that *ALVE6A* is located proximal to the 1p telomeric hotspot of recombination, the discrepancy between the chiasma-based and recombination-based genetic length of the 1p arm is bound to be even more.

The genetic length of the 1q arm ($W_{1cen-1qter}$) can be roughly approximated by the genetic linkage between proximally located *GAPD* and *PGR*. The latter was mapped in the subtelomeric part of 1q, within the 1q4.1–1q4.3 region (Dominguez-Steglich et al. 1992). The position of the 1q4.1–1q4.3 region on the map of LBC 1 is not distinctly determined to date, but the chiasma-based distance between the centromere and ITS16 site of the TTAGGG repeat that was mapped proximally to the *PGR* gene within region 1q3.3–1q3.5 is 155 cM. By all appearances, the 1q4.1–1q4.3 region carrying the *PGR* gene lies within the 1K–1L1 region (see Figure 6). It means that the crossover-determined distance between the centromere and the *PGR* gene should be within the limits of 162–251.5 cM. The genetic distance between *GAPD* and *PGR* ($W_{GAPD\text{-}PGR}$) estimated in genetic studies of the Compton reference population is 320 cM. Therefore $W_{1cen-1qter}$, the genetic length of the chicken 1q arm, which is determined as a sum of effects of all recombination mechanisms, is about 1.3–1.9 times more than the chiasma (crossing over)-determined genetic length of the arm. If the chiasma-based data presented in this article are compared to the genetic linkage data, one can see that the chiasma-based recombination ratio (0.649 Mb/cM) for chromosome 1 is much greater than the genetic-based recombination ratios (0.348 Mb/cM, 0.488 Mb/cM, 0.462 Mb/cM) estimated on the basis of the Compton, East Lansing; and Wageningen maps, respectively (see Smith and Burt 1998). Thus differences between experimental genomic estimated distances and chiasma-based genetic distances actually exist. The study of this phenomenon is of fundamental importance for chicken genome mapping.

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