Lampbrush Chromosomes of the Chicken, *Gallus domesticus*

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**Abstract.** We examined lampbrush chromosomes (LBC) prepared from chicken oocytes of 1–3-mm diam using both light and electron microscopy. Both macro- and microchromosomes form LBC with morphologies very similar to the well known newt and salamander LBC. In chicken LBC typical loops have a contour length of \( \sim15\ \mu m \), although some loops range up to 50 \( \mu m \). Multiple transcription units are present on some loops. Electron microscopic examination of Miller spread preparations reveals closely spaced nascent transcripts typical of LBC transcription. We used \( \textsuperscript{3}H \)-labeled chicken DNA as a probe for light microscopic level in situ hybridization to repetitive sequences associated with nascent RNA transcripts. Approximately 25 sites were labeled, primarily on the microchromosomes, plus sites on chromosome 2 and on the putative sex chromosome. The small genome size of the chicken (1.2 pg) presents a considerable advantage over that of newts or salamanders in further study of LBC structure and function.

**Lampbrush** chromosomes (LBC)\(^1\) are formed during oogenesis in many animal species. These highly extended, looped chromosomes are found in diplotene of meiotic prophase and are characterized by extensive transcription on the loops. An excellent review of LBC investigations and techniques has just been published by Callan (1986). This reference should be consulted for a more detailed discussion. Despite a century of study, we still know relatively little about the function(s) of these meiotic chromosomes, particularly with respect to the nature of the transcribed sequences and the control of their expression. Almost all that we do know about their organization and activity comes from investigations of newt and salamander LBC where the large genome sizes that favor cytological study are serious obstacles for experiments based on molecular biological and recombinant DNA techniques. Although LBC can be found in meiotic diplotene oocytes of many animal species, frequently the material is refractory to study. For example, the nuclear sap is very stiff and spreads poorly in some species, making good chromosome preparations very difficult to obtain. Acknowledging these problems, several workers in the field are exploring other animal systems that might prove suitable for both cytology and molecular biology. Gall and Callan and their colleagues, for example, have directed some efforts toward establishing *Xenopus laevis* as a suitable alternative system (Jamrich et al., 1983; Gall et al., 1983; Muller, 1974). Jamrich et al. (1983) recently demonstrated that despite the small chromosome and loop size, *Xenopus* LBC are suitable for analysis by in situ hybridization to nascent RNA transcripts.

Recognizing that the molecular organization of the chicken genome presents certain advantages over that of *Xenopus* (e.g., *Xenopus laevis* is essentially tetraploid; chickens have a smaller genome at 1.2 pg and very little repetitive DNA; numerous chicken genes are already cloned and characterized, particularly with respect to nuclease sensitivity and chromatin domain organization), we investigated the cytology of chicken oocyte LBC. As reported here, the chicken ovary is amenable to standard LBC methodology. Except for their smaller size, the organization of chicken LBC appears to be quite similar to the classical amphibian LBC (see Callan, 1986).

An interesting aspect of chicken cytology is the karyotype comprising both macro- and microchromosomes, a pattern that is typical for birds and reptiles. In early cytological studies, the microchromosomes were viewed as variable heterochromatic elements or as supernumerary chromosomes without typical genetic functions. Improved cytological technique helped establish the chromosome number for the chicken, *Gallus domesticus*, at 39 pairs, with the largest 9–12 pairs designated as macrochromosomes. In mitotic metaphase these macrochromosomes range from 2 to 10 \( \mu m \) in length. The remaining chromosomes are considered microchromosomes and represent \( \sim35\% \) of the total genome length (Kaelbling and Fechheimer, 1983). Several genetic functions including the nucleolus organizer, the major histocompatibility locus, several oncogenes, thymidine kinase, and endogenous viral loci have now been mapped to microchromosomes (reviewed by Somes, 1984; Bloom and Bacon, 1985) establishing that normal genetic functions are carried on the chicken microchromosomes. Furthermore, cytological study showed that kinetochores are clearly present on both mitotic and meiotic microchromosomes. In addition, during meiosis, normal synaptonemal complexes form on

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\(^1\) Abbreviations used in this paper: DAPI, \(4',6\)-diamidino-2-phenylindole dihydrochloride; GV, germinal vesicle; LBC, lampbrush chromosome(s); TU, transcription unit.
the microchromosomes (Solari, 1977; Kaelbling and Fechheimer, 1983) and the microchromosomes form typical LBC in oocytes. By all these criteria, the microchromosomes are normal, though diminutive, chromosomes and present some advantages and some disadvantages in the continuing investigation of chicken LBC.

We examined chicken LBC as an experimental system primarily to investigate several related questions of chromosome structure and gene regulation. (a) What genes are transcribed during the LBC stage of oogenesis? (b) How is transcription and the processing of transcripts regulated (see, for example, the read through transcription model, Gall et al., 1983). (c) What sequences map to the base of a loop? (d) Are these loop base sequences structural sequences that specify the limits of a domain regardless of cell type?

Materials and Methods

Lampbrush Chromosome Preparations

Detailed descriptions of methods used for lampbrush chromosome preparations are found in Callan (1986) and Macgregor and Varley (1983). The methods and buffers used here are those recommended by Gall et al. (1981).

All the manipulations of oocytes and germinal vesicles (GV) use the magnification of a dissecting microscope (12x and 50x).

White leghorn laying hens (usually less than 1-y-old) were obtained from College Biologicals, Bothell, WA or H & N Farms, Redmond, WA. After euthanasia of the bird, the ovary was surgically removed and stored without College Biologicals, Bothell, WA or H & N Farms, Redmond, WA. After the ovary with Dumont forceps and collected in Gall's 5:1 + PO4 buffer but not over 24 h. White egg follicles of ,x,3-mm diam were pulled from the well slide chamber, the nuclear envelope was manually removed from the well slide. Mell~l paraffin was used to seal the two slides together. In the well slide containing more of the latter buffer. The well slide was made by sealing a Clay Adams No. 4555 suction aid. The end of the capillary had been prepolished and constricted slightly in a Bunsen flame. Using the technique of Gall et al. (1981).

In Situ Hybridization

Dry slides were baked at 65°C for 0-2 h (Gall et al., 1981). The probe, total chicken DNA, was labeled with 3H by nick translation to 2 x 106 cpm/µg (counting efficiency ~30%) and heat denatured. The hybridization mix contained 40% deionized formamide, 4x SSC, 0.1 M NaPO4, pH 7, E. coli DNA at 300 µg/ml, and probe DNA (SSC is 0.15 M sodium chloride, 0.015 M sodium citrate, pH 70). Each slide was hybridized with 105 cpm of probe in a 5-µl drop under a coverslip sealed with rubber cement. The preparations were hybridized for 12-24 h at 37°C-38°C. After hybridization, the slides were rinsed in 1x SSC, then washed for 1 h in 1x SSC at 65°C followed by dehydration through 70, 95, and 100% ethanol. For autoradiography, the slides were dipped in Kodak NTB-2 emulsion and exposed at 4°C for 6 d to 3 mo. The emulsion was then developed for 2% min in Kodak D-19, rinsed in water, and fixed in Kodak Rapid Fixer for 2 min, all at 15°C. After extensive rinsing, the slides were first dried and then stained with Coomassie Blue as recommended by Gall et al. (1981).

DAPI Staining

Dry slides were stained for 5 min in 0.1 µg/ml 4,6-diamidino-2-phenylindole dihydrochloride (DAPI; Sigma Chemical Co., St. Louis, MO) in 1/4 5:1 + PO4 buffer. After rinsing and mounting, the slides were examined by epifluorescence with the Leitz Ortholux microscope using the G or A filter cube. The slides were photographed on Kodak Ektachrome 400 film push developed to 800 or Kodak Tri X film push developed to 1600 ASA.

Electron Microscopy

Details of the Miller spreading procedure are included in Callan (1986) and Macgregor and Varley (1983) and the literature cited there. For light and electron microscopy, the preparations were fixed in 70% ethanol and then stained with mouse monoclonal antibodies Y-12 (anti-Sm) or Y-28 (anti-DNA) diluted 1:50 in PBS-BSA (0.01 M NaCl; 0.2 % KCl; 2.16 g Na2HPO4 · 7H2O; 0.2 g KH2PO4, per liter pH 7.4, plus 1% BSA). Both antibody samples were provided by Joan Steitz at Yale University. The preparations were then washed and stained with fluorescein-conjugated secondary antibody (Sigma rabbit antimouse) diluted 1:1,000 in PBS-BSA. A Zeiss photomicroscope III with filter set 05 was used for examination of the slides, and the images were photographed on Kodak Ektachrome 400 daylight film push developed to 800 ASA.

Results

Since previous reports already indicated the existence of LBC in chicken oocytes, our first step was simply to determine whether reasonable quality chromosome preparations could be made from these. Lampbrush chromosomes of chickens were described initially by D'Hollander (1904). Koecke and Muller (1965) examined intact GVs from chicken oocytes of ~1-mm diam in an attempt to establish the chromosome number. Later Wylie (1972) described the development of LBC in his studies of ribosomal DNA and RNA synthesis in sectioned chicken ovary. Ahmad (1970) also studied chicken LBC and was the first to report that isolated chromosome preparations could be made, although the figures in his published manuscript were from intact GVs or ovary sections.

When we examined sections of ovary from a bird at 12 wk posthatching, we observed oocytes of ~0.13-mm diam containing early LBC, confirming the reports of both Wylie and Ahmad. Both Koecke and Muller (1965) and Ahmad (1970) showed that large LBC are present in egg follicles of 1-2-mm diam in the adult laying hen (laying typically begins around 21 wk posthatching). Oogenesis in the hen is asynchronous, and thus oocytes of all sizes are usually found in the adult ovary. Since oocytes smaller than 1-mm diam are too small
for easy manual LBC techniques, follicles of 1-3-mm diam from adult laying hens have been used in these studies. Fortuitously, LBC loops appear to be at their maximum extension in oocytes of this size range. By the time oocytes reach 3-mm diam, the LBC stage begins to decline and both chromosomes and loops begin to contract.

In making chicken LBC preparations essentially the same techniques developed for newt LBC can be used, particularly those of Gall et al. (1981). In comparison with the newt, Notophthalmus viridescens, chicken GV's are a bit smaller and somewhat more difficult to handle. In 1-3-mm chicken oocytes, the GV's usually range from 200 to 400 mm in diameter. The quality of chicken LBC preparations tends to be more variable from animal to animal and even among similar sized oocytes from the same animal relative to the newt. The spread chromosome preparations were examined “live” with an inverted microscope and phase-contrast optics or, more routinely, as dry preparations before in situ hybridization or as stained preparations after hybridization. From these observations it is immediately clear that both macro- and microchromosomes form typical LBC as loop-bearing paired chromosomes or bivalents (Fig. 1). The large chromosome number (2n = 78 chromosomes) and the small size of the chicken GV's usually range from 200 to 400 mm in diameter. The quality of chicken LBC preparations tends to be more variable from animal to animal and even among similar sized oocytes from the same animal relative to the newt. The spread chromosome preparations were examined “live” with an inverted microscope and phase-contrast optics or, more routinely, as dry preparations before in situ hybridization or as stained preparations after hybridization. From these observations it is immediately clear that both macro- and microchromosomes form typical LBC as loop-bearing paired chromosomes or bivalents (Fig. 1). The large chromosome number (2n = 78 chromosomes) and the small size of the microchromosomes present some disadvantages here. Rarely can all 39 chromosome bivalents be found or identified within a single spread. As with many amphibian species, the centromeres are not obvious on the chicken LBC. Despite these problems, some chromosome bivalents and an apparently unpaired univalent are readily identified in most preparations based on chromosome size and presence of “landmark” structures (Fig. 2 and 3). Landmark structures include loops of unusual size or morphology, knobs, spheres, and fused loops (see Callan [1986] for further information). Chromosome 1 (the largest with chromosomes numbered in order of decreasing size) has enlarged floucy loops at one end, and at the opposite end the telomeres are nearly always fused (Fig. 2, open arrowheads, bottom and top of chromosome 1, respectively). Chromosome 2 has a paired densely staining landmark in a subtelomeric position and large loops at the opposite end (Fig. 2, top and bottom arrowheads on chromosome 2). One microchromosome carries a set of very dense loops (microchromosome in Fig. 1 and Fig. 3 c).

A chromosome that we have tentatively identified as a sex chromosome is easily recognized in these preparations as an apparently unpaired chromosome (Fig. 2 and 3). The size of this chromosome is consistent with a tentative identification as the Z chromosome. This chromosome has a striking landmark loop-bearing knob near one end that varies in morphology from a condensed knob to a very extended loop structure (Fig. 2). The opposite end of this chromosome often has a small distinct set of loops. In general, loops on this chromosome seems less extended than those on other chromosomes in the same spread.

Chromosome length and loop size are a function of the stage in the progressive formation and retraction/compaction process as diplotene progresses and the oocyte grows. In chromosomes that appear to be at or near maximum loop extension, chromosome 1 is 150-μm long. Contour lengths of typical loops range from 10 to 15 μm although some loops extend up to 50 μm in contour length. The actual packing form of the DNA in these preparations is unknown, but for purposes of estimation, 1 μm of B-DNA equals 3,000 base pairs. Thus a typical loop contains an estimated 30,000-45,000 base pairs.

In the currently accepted view of newt LBC organization, transcriptionally active LBC loops represent ~5-10% of the DNA, with the rest of the chromatin packaged into condensed chromomeres forming the chromosome axis. To examine the distribution of DNA in chicken LBC, we stained the chromosomes with the DNA-specific, fluorescent dye, DAPI. The fluorescence patterns give a very striking view of the chromomeric organization of the chromosome axis, consistent with the bulk of the DNA being present in chromomeres (Fig. 4 a). Many of the microchromosomes exhibit a pair of particularly bright terminal chromomeres when stained with DAPI (Fig. 4, a-c). The landmark structure of the putative Z chromosome also fluoresces very strongly with DAPI staining (Fig. 3, b and c).

Since the amount of DNA in a loop is very small, the loops are very faint with DAPI staining although there are occasional small points of brighter fluorescence scattered along the loop axis, which many represent untranscribed, condensed DNA within the loop axis (Angelier et al., 1986). Essentially the same staining patterns were observed when the LBC were examined by indirect immunofluorescence staining with an anti-DNA monoclonal antibody. The example shown in Fig. 5 a reveals chromomeric staining with anti-DNA while Fig. 5 b shows a portion of a chromosome stained with anti-Sm (specific for proteins in snRNP particles) for comparison. The anti-Sm antibody labels the nascent transcripts on the loops. (The photographic exposure used in Fig. 5 a reveals only the chromomeric pattern and not the punctate loop fluorescence.)

Loop and Transcription Unit (TU) Morphology in Electron Microscope Spreads

Since we anticipate using chicken LBC in a number of experiments requiring in situ hybridization to nascent transcripts along transcribed loops, it was important to establish that the loop matrix actually contains RNA transcripts and in sufficient numbers to present a reasonable target for the

Figure 1. Montage photograph of chicken lampbrush chromosomes showing a macrochromosome and, in the insert at lower left, a microchromosome at the same magnification. Typical loops are present on both chromosomes. Phase-contrast optics. Bar, 20 μm.
Figure 2. Examples of chromosomes 1 and 2, the putative sex chromosome, and several unidentified microchromosomes demonstrating some of the landmark structures used in chromosome identification as well as some of the sites labeled by in situ hybridization with ³H-labeled total DNA as a probe. Hybridization with this complex probe is expected to label transcripts containing repeated sequences. The probe hybridizes to the nascent RNA transcripts; the DNA in the chromosomes is not denatured. In the whole lampbrush chromosome karyotype ~25 sites are labeled, primarily on the microchromosomes plus a few macrochromosome sites. In the examples shown, the
hybridization. Preliminary experiments using acridine orange staining and also \( ^{3}H \)uridine incorporation followed by autoradiography indicated the presence of active RNA transcription on the loops (results not shown). To confirm the nature of the loop structures we prepared specimens for the electron microscope using both standard Miller spreading techniques and modifications, which preserved more of the chromosome structure.

In Situ Hybridization to Chicken LBC

To test the general feasibility of in situ hybridization to chicken LBC transcripts, total DNA was tritium labeled by nick translation and used as probe. In this protocol, chromosomal DNA is not denatured; DNA/RNA hybrids form on the nascent transcripts present on the loops. The probe used here was expected to detect only repeated sequences present in transcripts. With exposures as short as 6 d the autoradiographic silver grains were localized over \( \sim 25 \) sites primarily associated with the microchromosomes, the putative sex chromosome, and on the subtelomeric landmark structure on chromosome 2 (Fig. 2). Stefos and Arrighi (1974) previously hybridized \( ^{3}H \)cRNA complementary to low Cot DNA to chicken mitotic metaphase chromosomes. They observed autoradiographic label primarily over the centromeric heterochromatin of microchromosomes and on the W chromosome. A few sites on macrochromosomes
Figure 5. Indirect immunofluorescence of chicken lampbrush chromosomes stained with primary monoclonal antibodies and FITC-labeled secondary antibodies. The chromosome in a was stained with an anti-DNA antibody revealing the beaded chromomeric axis of the bivalent. For comparison, the chromosome in b was stained with an anti-Sm antibody, which labels the nascent RNP complexes on the loops. Bar, 10 μm.

were evident on longer exposures. Thus the pattern observed here by transcript hybridization is generally consistent with their results on repetitive DNA distribution. Among the microchromosomes, the labeling was usually at a single site on each half bivalent and frequently this pair of labeled sites was at or near a chromosome end (Fig. 2). A few microchromosomes were unlabeled, whereas others showed two paired sites of hybridization (not shown). In a few cases hybridiza-

Figure 6. Electron micrographs showing the structure of the loops and the transcription units from chicken lampbrush chromosomes. In a–c, the preparations have been only slightly dispersed. Multiple transcription units in the form of thin-to-thick gradients of RNP loop matrix are present on several loops. (d) The chromatin is more dispersed in this preparation revealing the high density of individual nascent transcripts along the loop axis. (a–c) Bar, 5 μm. (d) Bar, 1 μm.
tion sites appeared to be heterozygous with labeling present on only one of the chromosomes in the bivalent (not shown). The landmark structure on the univalent (sex) chromosome usually shows some labeling (Fig. 2). With long exposures some additional sites begin to show labeling, but these minor sites have not been mapped so far. Most of the other prominently staining landmark structures were not labeled above background.

The landmark structure on chromosome 2 labeled by the total DNA probe probably contains a GC-rich repetitive sequence. Hybridization occurs at this same site with a cloned gene probe containing GC tails used in cloning. Hybridization with [$^3H$]poly(dG).poly(dC) also labeled this site, whereas the cloned gene sequence minus the region with GC tails did not hybridize to this site (data not shown).

Discussion

Lampbrush chromosomes present a unique opportunity to study transcriptionally active chromosomes. Previous studies primarily used newts and salamanders because their chromosomes are very large, consistent with their large genome sizes (20–100 pg). However, large genomes, especially those with many repetitive sequences, present numerous problems in the application of current recombinant DNA technology. As an alternative, chicken oocytes contain typical although smaller LBC as predicted from the smaller genome size (1.2 pg haploid).

As demonstrated here, chicken LBC have essentially the same structure as the better known newt and salamander chromosomes, and they are quite suitable for studies of gene expression using in situ hybridization to nascent transcripts or analysis by immunofluorescence. As a test to show that chicken LBC are suitable for analysis by in situ hybridization, we used total DNA as a probe. Due to the complexity of the probe, we expect that only repetitive sequences present in transcripts would be significantly labeled. Since repetitive sequences have been previously detected in various amphibian LBC loop transcripts (see for example Jamrich et al., 1983, and Callan, 1986), this type of probe was very likely to give a positive signal. The total DNA probe did in fact hybridize to numerous sites and in a pattern consistent with the known general distribution of repetitive sequences in the chicken genome. (Note that the hybridization to transcripts can only detect sequences within the estimated 5–10% of the genome that is expressed during LBC transcription.)

One unusual chromosome appeared to be an unpaired chromosome or univalent. In chickens, the female is the heterogametic sex having a ZW chromosome constitution (males are ZZ). The Z chromosome is about the fifth largest chromosome whereas the W is about the size of chromosome 10. The observed univalent was about the right size or a little smaller than that expected for the Z chromosome. No obvious candidate for the W chromosome was identified, possibly because the W may be difficult to recognize among the microchromosomes. However another possibility is that the W chromosome is present associated with the Z through one point of pairing. There is a region at one end of the putative Z that stains intensely with DAPI and is very often densely stained by Giemsa or Coomassie forming a landmark structure. Solari (1977) previously demonstrated that the Z and W do pair during early prophase, but it is not known if they remain paired. The identification of a W chromosome specific repetitive sequence by Tone et al. (1984) provides an approach to identifying the W and answering this question.

The chicken karyotype does contain microchromosomes that are troublesome in their small size and large number at the light microscope level, but they also present opportunities for gene mapping by pulse-field electrophoresis and for more thorough ultrastructural study at the electron microscopic level. We are currently working to exploit these advantages.

Many of the findings reported here on chicken oocyte LBC and TU morphology closely parallel the results of Gaginskaya and colleagues (Kropotova and Gaginskaya, 1984; Tzvetkov et al., 1984) with Japanese Quail oocytes and LBC. These authors note that they were unable to find amplified nucleoli in quail oocytes; similarly we did not identify any amplified nucleoli in chicken oocytes. This result is interesting since [$^3H$]thymidine incorporation studies by Wylie (1972) indicated DNA synthesis in the nucleolus at a time that is typically associated with ribosomal gene amplification in other animal species. Further investigations will be needed to determine if amplified nucleoli are present.

The nature of LBC transcription units is currently under study in several laboratories. Gall et al. (1983) recently suggested that LBC transcription termination occurs only as a consequence of TUs running into each other or into the chromosome. The DAPI and anti-DNA loop staining patterns observed here may be inconsistent with this model. With either staining procedure loops were generally very faintly stained but also contained numerous punctate fluorescent sites. One interpretation for these fluorescent sites would be the presence within loops of untranscribed, condensed DNA between transcription units on an extended loop. We are attempting to establish a complete map for a single loop to further test this model.

Many chicken genes have been cloned and characterized, making it relatively straightforward to now approach several interesting questions of LBC function, particularly to ask what kinds of genes are transcribed on LBC loops. We have used several cloned chicken gene probes in transcript hybridization and surprisingly, obtained essentially negative results. Substantiation of these negative results requires a positive single copy gene hybridization probe to be included in each hybridization. Recently, we identified such a sequence by analyzing pools of lambda clones containing chicken genomic DNA. We are continuing to map and study this clone as well as using it as a standard in the experiments mentioned above. From this clone we do know that we can detect LBC transcripts of a single copy sequence. The average LBC loop size in chickens is ~10–15 μm or roughly 30,000–45,000 base pairs. This size is easy to cover in a "chromosome walk" making it feasible to map an entire loop and hence, to correlate map position to DNA sequence distribution.

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