Lampbrush Chromosomes of the Chicken: Cytological Maps of Macrobivaients

L.A. Chelysheva, I.V. Solovei, A.V. Rodionov, A.F. Yakovlev, E.R. Gaginskaya

Biological Research Institute. Leningrad University and the All-Union Research Institute of Farm Animal Breeding and Genetics, Leningrad

The morphology of lampbrush chromosomes of the chicken has been studied. We identified six pairs of autosome bivalents and the sexual ZW-bivalent. The cytological map of the lampbrush macrobivalents have been constructed.

The modal number of chromosomes in the karyotypes of birds is 80, but, as a rule, only five or six pairs of the largest chromosomes referred to as macrochromosomes are possible to identify on chromosome preparations (Bulatova, 1977; Srb, Pusa. 1986). The term "macrochromosome" should not cause confusion: The length of the largest of macrochromosomes in metaphase is no more than 5-6 μm (see: Srb, Pusa, 1986). The size of some microchromosomes during metaphase is such that they are hardly visible on the maximum resolution of a conventional microscope. These particularities of bird karyotypes place rigid limitations on the prospects of applying cytogenetic analysis to study the evolution of karyotypes (Bulatova, 1977; Stock, Bunch, 1982) and mutagenesis (Bloom, 1981). They are the fundamental cause of the difficulties that researchers encounter when trying to map the genes of birds by methods of DNA hybridization *in situ* (Palmer, Jones. 1986) and blot hybridization with fractionated chromosomes (Hughes et al, 1979; Stubblefield, Oro, 1982).

It is possible to increase the capacity of cytogenetic analysis if one works with weakly condensed chromosomes. Usually to delay the condensation of the chromosomes, chemical agents are used, such as methotrexate, BrdU or ethidium bromide. Using this approach, weakly-condensed chicken chromosomes were described, of which 16 pairs of homologs were identified (Carlenius et al, 1981; Sasaki, 1981).

However, a principally different approach is possible. Chromosomes in the growing bird oocytes are known to be at the lampbrush chromosome stage (Loyez, 1906; Gaginskaya, 1972). At the previtellogenesis stage, they have a length of up to 400 micrometers as, for example, the pigeon chromosome 1 (Khutinaeva et al, 1989a, 1989b). Recent studies of bird lampbrush chromosomes (LBCs) and attempts to map physically some cloned sequences transcribed in oogenesis on these chromosomes showed that only 2-3 autosomes and sex bivalent can be undoubtedly identified in the previtellogenesis oocytes of the chicken (Kropotova, 1984; Hutchison, 1987; Gaginskaya, 1989; Rodionov et al, 1989; Tarantul et al. 1989b). In this work we describe of six autosome bivalents and the sex bivalent, and also present detailed cytological map of the chicken lampbrush macrochromosomes.

Materials and Methods

The LBCs were taken from oocytes of a diameter of 0.75-2.75 mm taken from adult hen of the "Zarja 17" cross, kindly supplied to us by Dr. L.A. Alekseevich (Department of Genetics of Leningrad University). The preparations were taken by the method initially developed for the LBCs of amphibians and modified for the chromosomes of bird oocytes (Kropotova, Gaginskaya, 1984; Hutchison, 1987). Two variations of the method were used. In the first, the nuclei from the oocytes were isolated in a medium containing 75 mM KCl and 25 mM NaCI in a ratio of 3:1, and for the isolation of the chromosomes and their dispersion we used TBS buffer of the following composition KCl – 80 mM,

NaCI – 20 mM, $MgCl_2$ (Sigma) – 1 mM, $CaCl_2$ (Merck) – 0.05 mM, Tris (Sigma), pH 7.0-8.0 – 20 mM (Kropotova, Gaginskaya, 1984). However more LBC morphology richer in detail was reproduced with the variation where the nuclei were isolated in the medium of Gall et al. (1983) KCI – 83 mM, NaC1 – 17 mM, Na_2HP0_4 (Merck) – 6.5 mM, KH_2P0_4 (Merck), pH 7.0-7.4. – 3.5 mM. The dispersion of the nuclear sap was done in the same medium diluted 1.33 times, with the addition of paraformaldehyde (Serva) to a final concentration of 0.1%.

The isolated chromosomes were centrifuged for 10-15 minutes at 700-1000 g for their application to slides, then fixed with 70% ethanol or 2% glutaraldehyde (Reanal), and stained with Giemsa or Coomassie Blue R-250 (Merck), dried and mounted in Canada balsam (Serva).

We conducted the chromosome morphometry on the photo prints with magnification 1000x using a curvometer. "Double bridges" which are extended lateral loops (Callan, 1986) were excluded from calculations when measuring the length of bivalent axes and the coordinates of marker structures.

Results

To isolate the bird LBCs, the diameter of the oocytes from which the nuclei are isolated is very significant. The optimal size of chicken oocytes from which LBCs with well spreaded loops are obtained is in the range of 0.5-1.5 mm. It is practically impossible to isolate nuclei from oocytes with a diameter of less than 0.5 mm. In oocytes with diameter 2.0 mm and larger, the LBCs are condensed: the bivalent length is reduced, most loops appear curled up. However, for finding marker loops the study of LBCs from oocytes of the diameter 2.5-3.0 mm may be useful, since with a background of curled ordinal loops, marker loops with massive RNP-matrix are more clearly visible.

LBCs isolated from the nuclei of chicken oocytes with a diameter of 0.75-1.5 mm are shown in figure 1-26. The bivalents are distinguished by their length, by their morphology and by the distribution of lateral loops, chiasmata, and "double bridges" along the axis of the chromosome. Aside from the primary mass of normal loops, the chicken LBCs contain several types of marker structures, some of which are analogous with the markers described earlier in the amphubian LBCs of amphibians (see: Callan, 1986). Thus for the consistency of description in the study of chicken LBCs, we use (where it's possible) the terminology developed for amphibian LBC.

Types of marker structures in chicken LBCs. "Lumpy" loops (LL-type) are loops usually found in a curled state and the appearance of lumps with irregular form (Figs. 2, 3, 7). The dense RNP matrix of the LLs are strongly stained with Coomassie and Giemsa (Figs. 10, 11, 13). After staining with acridine orange (Rodionov et al, 1989) they are distinguished by a bright red color beside the green chromomeres and pink ordinal loops. Among the LLs stand out giant lumpy loops (GLL) of the sex bivalent (Figs. 7, 20-22). LLs are convenient and reliable markers.

A special type of telomeric loops, called "fluffy" by Hutchison (1987) are observed on the telomeres of the largest chromosomes and some microbivalents (Figs. 1-19). They are not described in amphibians and will be referred to as telomeric bow-like loops (TBLs). As a rule, these loops are found on the preparations in a relaxed state (for example, see Figs. 1 a; 8), but less frequently in some bivalents and more so in others they can be curled (Figs. 1 c; 9). In some of the macro- and microbivalents the telomeres on the place of the bow-like loops contain curled loops with a dense, intensively stained matrix (Figs. 5, 6; 7, d). We call them as telomeric giant lumpy loops (TGLs). These loops were never completely relaxed on our preparations; usually they were curled.

TBLs and TGLs are found only on one of the telomeres of all chicken LBCs. The opposite telomere appears as a lump of chromatin and (at least in some cases) has a small lumpy loop (Figs. 4, 5, 16, 17).

Among the loops of interstitial regions of bivalents are found large loops (up to 60 μm in length) of the normal type, some of which can be identified on chromosomes of different oocytes thanks to their unusual length. We refer to such loops as "marker loops" or MLs. MLs are particularly easy to identify in oocytes where most loops for one reason or another are curied (see figures 8 and 9).

Experience of the work with chicken LBCs shows that dependable and convenient markers for the chromosome regions can be found with the clusters of adjoining chromomeres lacking pronounced loops, reminiscent of the centromeric "bars" of amphibian LBCs (Callan, 1986). The length of such "loopless" regions can attain 10 μm. On a chromosome can be found one (Figs. 3-6). two (Fig. 2, 7), or three (Fig. 1) of such loopless chromomere clusters. Moreover, the arrangement of the most visible of these coincides with supposed location of the centromere at the base of the centromeric index of the chromosomes (see below). For the convenience of description the boundaries of the "loopless" section are considered the first looped chromomeres adjacent to it. and the corresponding loops are named in relation to their location relative to the middle of the bivalent as the proximal and distal boundary loops (PBLs and DBLs).

In this manner, when describing the chicken LBC we distinguish the following marking structures and use the following designation: LL-lumpy loop, GLL-giant lumpy loop, ML-marker loop, GML-giant marker loop,. DBL-distal boundary of the loopless region, PBL-proximal boundary of the loopless region. T-telomere, TBL-telomeric bow-like loop, TLL-telomeric lumpy loop, TGL-telomeric giant lumpy loop.

Bivalent A (probably chromosome 1 of the chicken karyotype; fig. 1, 8. 9). This is the longest chromosome in all the oocytes that were studied. On our preparations the average length of this chromosome was 185 μm. This bivalent exhibits 7.3 ± 0.2 chiasmata that distributed along the chromosome not altogether randomly (one of the telomeres in bivalent A, as a rule, is closed with a chiasma). The procedures for readying the preparations usually do not violate the integrity of the axis of bivalent 1; the extensive double bridges were not visible on it.

On the bivalent A were revealed 14 markers, the coordinates for 13 of them have been included in Table 1. The bivalent is identified by the characteristic, almost always relaxed telomeric loops TBL11, by a chiasma, usually located on the telomere T12 (less frequently next to it), and by the characteristic group of loops (usually a triplet), adjoining this telomere. The coordinates of the last marker were not determined, since it was difficult to define a single boundary of this group of loops while comparing the bivalents of various oocytes. On the bivalent there are at least three loopless regions most visible of which was flanked by loops PBL12 and DBL12. Aside from the markers already indicated, we will note loop PBL11 in the middle of the bivalent, especially noticeable on the relatively condensed bivalents from large oocytes. The length of the lateral loops in different sections of the bivalent varied (Fig. 1), the drawing of alternation of sections with long and short loops is an important diagnostic indication in this and other chicken LBCs.

Bivalent B (probably chromosome 2 of the chicken karyotype; Fig. 2, 10, 11). The average length of the bivalent on our preparations is 151 mkm (81% of the length of bivalent A). The average frequency of chiasmata in the bivalent is 5.5 ± 0.2. There are also no "double bridges". 12 marker structures are found, the coordinates of which are defined (Table 1). The chromosome is identified by the characteristic lumpy loops LL21 and LL22. In this bivalent, as a rule, the loop LL22 of homologous chromosomes are

fused. Beside the TBL21 loop a chiasma is often found, and there is no chiasma on the opposite telomere, as is characteristic feature of bivalent A.

Bivalent C (probably chromosome 3 of the chicken karyotype; Fig. 3. 12, 13). The average length of the bivalent in our preparations is 128 μm (69% of the length of bivalent A). The average number of chiasmata is 4.7 ± 0.2. 7 markers were identified the coordinates of which are defined (Table 1). The bivalent is identified by rts characteristic lumpy loop LL32, that some time is relaxed, the loopless region adjoining telomere T32. and the characteristic distribution of loops along the chromosome: marker ML33 divides the chromosome into two approximately equal areas, that are distinguished by the length of the loops (in the section ML33-T32 the loops are noticeably smaller).

Bivalent D (probably chromosome 4 of the chicken karyotype; dFig. 4, 14, 15). The average length of the bivalent is 107 μm (35% of the length of bivalent A). The bivalent has an average of 3.8 ± 0.3 chiasmata. The coordinates of the six markers are defined (Table 1). The chromosome is poorly preserved on the preparations, it is often separated by "double bridges" into fragments. The telomeric bow-like loops are poorly displayed. They are adjoined by the region where curled loops predominate. This region is bordered by marker loop ML41, the first large loop in a series of relatively long loops, occupying the center of the bivalent. It is namely here that "double bridges" are formed on the LBCs. Among the loops of this region the large loops of ML-42 stand out. the entire length of which occupies one transcriptional unit. The distinct loopless region is flanked by the loops PBL41 and DBL42.

Bivalent E (probably autosome 5 of the chicken karyotype; Fig. 5.16,17). The average length of the bivalent is 72 μm (39% of the length of bivalent A). This chromosome has an average of 2.5 ± 0.1 chiasmata. The coordinates of the five markers are defined (Table 1). The axis of the chromosome is always fragmented by "double bridges." On some of the preparations it can be seen that the telomeric loops have a large contour length and contain much RNP-matrix. but they are bent and appear as typical lumpy loops as a rule. The characteristic features of bivalent E are these loops (TLL51 or TGL51) and the loopless section separated by the "double bridge" adjoining telomere T52.

Bivalent F (Fig. 6,18-19). It is impossible to simply correlate this bivalent with a particular chromosome of the standard karyotype of the chicken (see, for example, Stock,. Bunch, 1982). Thus, in naming the markers we maintain the letter F, but note that there are reasons to suppose (see the section. Discussion) that bivalent F corresponds to a submetacentric chromosome of karyotype 8 of the chicken. The length of the bivalent is 36.5 μm (20% of the length of bivalent A). All bivalents. identified by us as bivalent F, have two chiasmata. The characteristic feature of this bivalent are the long multiple loops adjoining one of the telomeres (marker GMLF1). A cluster of loopless chromomeres, flanked by loops PBLF1 and DBLF1, is in the middle section of the chromosome. Telomeric loops are usually relaxed, only in some of the preparations they have the appearance of large lumpy loops.

Sex Bivalent ZW (Fig. 7, 20-22). The sum length of the Z and W chromosomes at the lampbrush stage is 64 μm. Like several microbivalents with terminal chiasma (see fig. 26, for example), bivalent ZW has a stick-like form, but unlike microbivalents it is asymmetrical. and has typical bow-like loops on one telomere and a giant lumpy loop on the other chromosome end. We were unable to map the chiasma, that is, to define the boundaries of the Z and W chromosomes. But, on the basis of observations of Solari and co-workers, it is appeared that this bivalent has a terminal chiasma (see: Rahn, Solari, 1986; Solari et al, 1988).

On this bivalent were found several loopless regions, one of which adjoins loops TBL-

ZW1, the second is approximately in the middle of the bivalent, and the third is at the base of the giant lumpy loops GLL-ZW1 and is visible only when a little RNP matrix is accented on the loop (Fig. 20-22).

Microbivalents (Fig. 23-26). Some of them have an interstitial chiasma, but most are coupled on account of the telomeric chiasma. The difficulties of identification microbivalents are tied to the fact that we were unable to preserve a complete oocyte chromosome set on our preparations. But several types of marker structures were observed in the microchromosomes, and it is possible to think that at least some of them can be identified in future. This is becoming especially interesting, if we look at the smallest microbivalents (for example, see Fig. 24). If the degree of decompactization of microchromosomes at the LBC stage is the same as the decompactization of macrochromosomes. then the length of smallest-microbivalents should be 30 times smaller in the metaphase of mitosis, like those shown on Fig. 24 (see also Table 2). about 0.1 mkm, and it is possible that they are not visible in metaphase.

Discussion

To find the correspondence between the described chicken LBC-macrobivalents and chicken mitotic chromosomes (Sasaki, 1981; Stock, Bunch, 1982; Rodionov et al, 1987; Auer et al, 1987) is a complex task. since the degree of condensation of both different chromosomes or chromosomal segments in mitosis and meiosis can vary (for example see Luciani et al. 1988; Khutinaeva et al. 1989a, 1989b), but, in general, the experience of work with amphibians (see Callan's survey, 1986) and birds (Kropotova, Gaginskaia, 1984; Gaginskaia, 1989; Khutinaeva et al, 1989a, 1989b) shows that linear correspondences between size of mitotic chromosomes and LBCs as well as their centromeric indexes (CIs) are usually observed.

Both CIs and lengths of LBCs (we note that the indicated length of LBC do not include that of the lateral loops and "double bridges"), the lengths of mitotic chromosomes in metaphase (Ermatov, 1983), the lengths of synaptonemal complexes in the pachytene of chicken meiosis (Rahn, Solari, 1986; Solari et al, 1988) are presented on Table 2. The definition of CI of the chicken LBCs demands a comment. Unfortunately, unlike the chaffinch (Gaginskaia, 1989) and the pigeon (Khutinaeva et al, 1989a, 1989b), the centromeric regions of chicken LBCs are not marked by specific structures, the so-called protein bodies. Earlier the hypothesis had been advanced that the centromeres of chicken LBCs are distributed within the boundaries of the clusters of loopless chromomeres (Rodionov et al, 1989), i.e. in areas bordered by the markers PBL12 - DBL12, PBL22 - DBL22, PBL31 - T32, PBL41 - DBL41, PBL51 - T51, PBLF1 -DBLF1, and PBLZW1 - DBLZW1. Analogical structures are described in the centromeric regions of the LBCs of several amphibians (Callan, 1986; MacGregor. 1986). It is appeared that they are centromeric C-heterochromatin bands and/or adjoining chromosome regions (idiograms of the C-bands of the chicken chromosomes: Pollock, Fechheimer, 1981; Rodionov et al, 1984, 1987). On the basis of this hypothesis several CI of the chicken LBC-macrobivalents are included in Table 2. They coincide well with the CI of mitotic chromosomes (Ermatov, 1983) and with the CI determined for chromosomes found in the pachytene stage (Rahn, Solari, 1986; Solari et al, 1988).

Judging from the relative length of the chromosomes and CI, bivalents A-E correspond to autosomes 1 -5 of the chicken karyotype. If our hypothesis about the location of the centromere in bivalent F in the area bordered by the markers PBLF1 and DBLF1 is correct, then this bivalent is formed by submetacentric chromosome 8, not the acro- and sub-acrocentric chromosomes 6 and 7.

In some bivalents at the LBC stage is observed more than one cluster of the loopless chromomeres (Fig. 1, 2, 7). It is logical to suppose that the additional loopless regions

must correspond to the interstitial C-bands. There is no direct evidence of the existence of such segments in the chicken macrochromosomes. but one should take into account that for some reason the C-heterochromatin of the chicken mitotic chromosomes is difficult to staining (Pollock, Fechheimer, 1981). The constant adhesion of the sister chromatides of chicken macrochromosomes in mitosis indirectly indicates the presence of interstitial heterochromatin in chicken chromosomes. As is known, the adhesion of heterochromatin segments of sister chromotides is one of the clearest properties of heterochromatin, permitting the identification of even small heterochromatic bands that are not cytochemically identified (Smaragdov, 1978; Smaragdov et al. 1980). We also note that the interstitial C-bands appear in the peacock chromosome 1 and 2, and in guineafowl chromosomes 1 and 4. The both species are karyotypiclly and philogenetically close to the chicken (Stock, Bunch. 1982).

It is interesting to discuss the nature of other markers used by us for the identification of LBCs. If the hypothesis of Zatsepina et al (1985) is correct about the loops of LBCs representing extended chromomeres of the G-bands, then the marker loops should correspond to the relatively large chromomeres of the G-bands of mitotic chromosomes. In this case, the long loop regions should be relatively inert genetically (Rodionov, 1985).

On the basis of nucleotide-specific fluorochromes staining of chicken LBCs (Rodionov et al, 1989), it was suggested that TBLs and probably LLs are arisen in telomeric, GC-rich heterochromatin that are visible on the telomeres of metaphase chromosomes (Rodionov et al. 1984.1989; Auer et al, 1987). The enrichment of loops LL21 and LL22 with GC-rich sequences can be suggested on the basis of the results of Hutchison who showed that these loops hybridize with probes containing poli(dG)-poli (dC)-sequences (Hutchison. 1987).

Attention is drawn to the mutual distribution of the pericentric clusters of loopless chromomeres and telomeric marker loops TBL and TGL. In complete accordance with the conception of "the chromosomal fields" of Lima-de-Faria (1983) TBLs and TGLs in all chicken macrobivalents are on a long arm, at the time when the opposite telomere is presented by a chromomeric granule and/or a small LL. The biologic mechanisms of this characteristic pattern is unclear.

Still one type of LBC markers, the "double bridges" represent lateral loops stretched at the base (Callan, 1986). The absence of "double bridges" in bivalents A, B, and ZW, as well as the contrary constant extension of bivalents E and F, and large microbivalents shows that the structural stability of either hypothetical “clips” at the base of lateral loops (Zatsepina et al, 1985; Gaginskaia, 1989), or of the hypothetical "skeleton" (Gasser, Laemmli, 1987) is different in different LBCs.

In conclusion, we stress that the unique cytological characteristics of bird LBCs, as well as the giant size, the distinct marker heteromorphism, the veriability of marker structures in philogenesis (Kropotova, 1984; Hutchison. 1987; Gaginskaya, 1989; Rodionov et al, 1989). permit one to use bird LBCs both in studies of various kinds of karyotype variability and in genetic mapping, the precision of which should be significantly better than the results obtained by working with mitotic chromosomes.

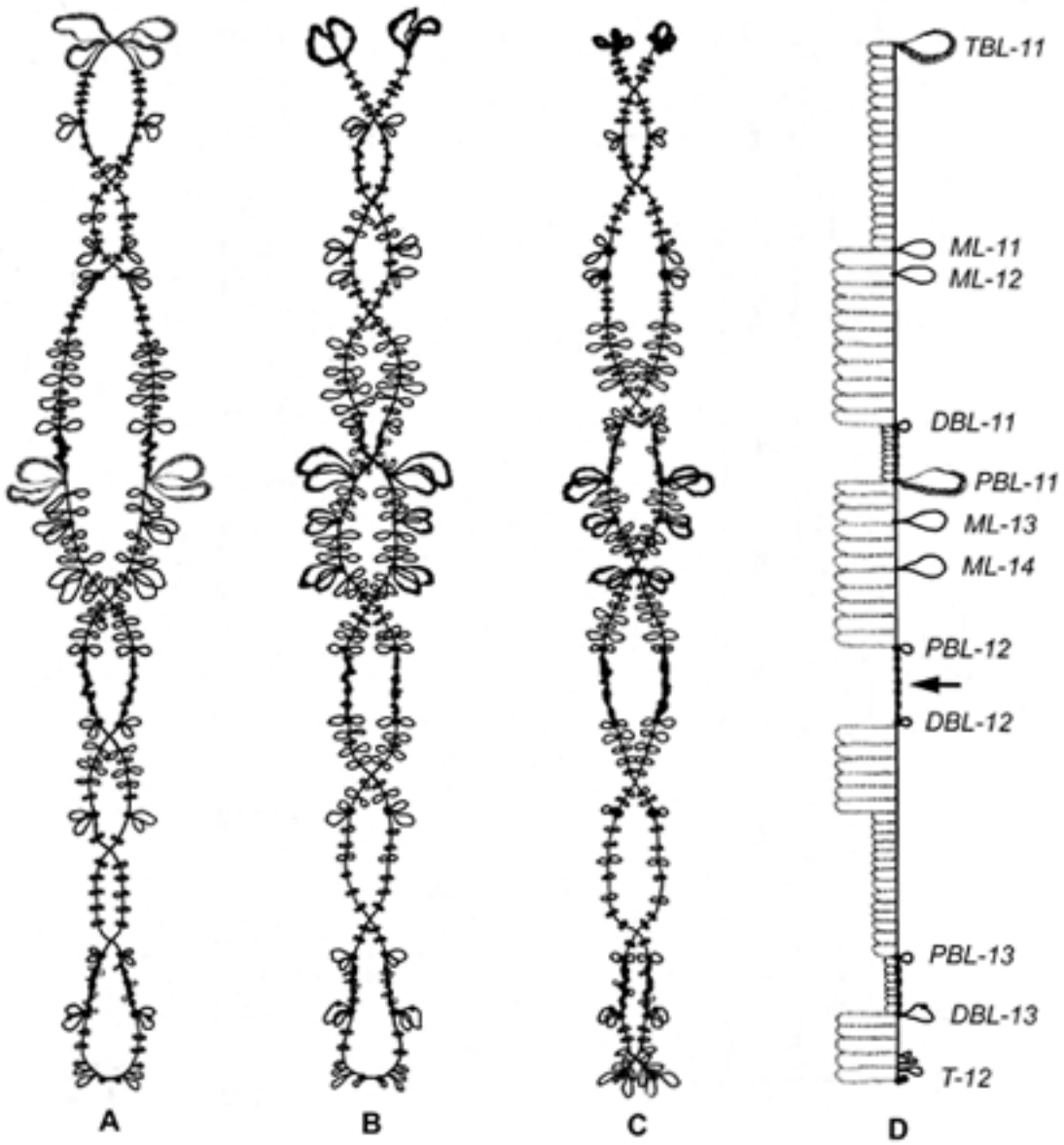

Figure 1. Schemes and a working map of the chicken bivalent A. **a-c**) schemes demonstrating the polymorphism of loops and chromomere pattern of the bivalent A. **d)** a working map of bivalent A showing the distribution of marker structures along the chromosome and the average length of normal loops in various parts of the chromosome. In this and subsequent figures the following designations of chromosome markers: LL-lumpy loops, GLL-giant lumpy loops, ML-marker loops. GML-giant marker loops, DBL-distal boundary of a loopless section, PBL-proximal boundary of a loopless section, T-telomere with small loops, TBL-telomeric "bow" loops, TLL-telomeric lumpy loops, TGL-telomeric giant lumpy loops.

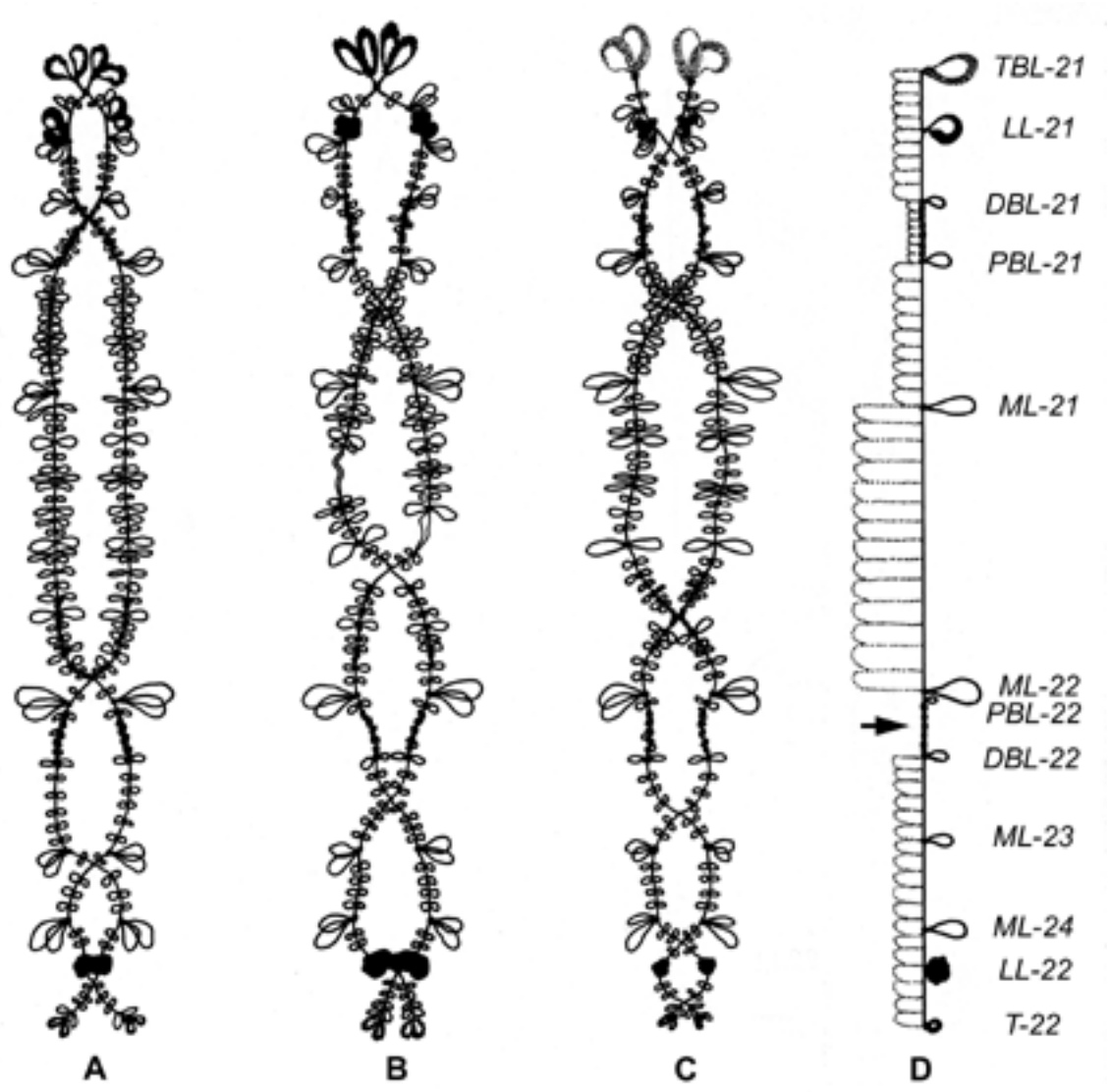

Figure 2. Schemes and a working map of the chicken lampbrush bivalent B. Descriptions see fig. 1.

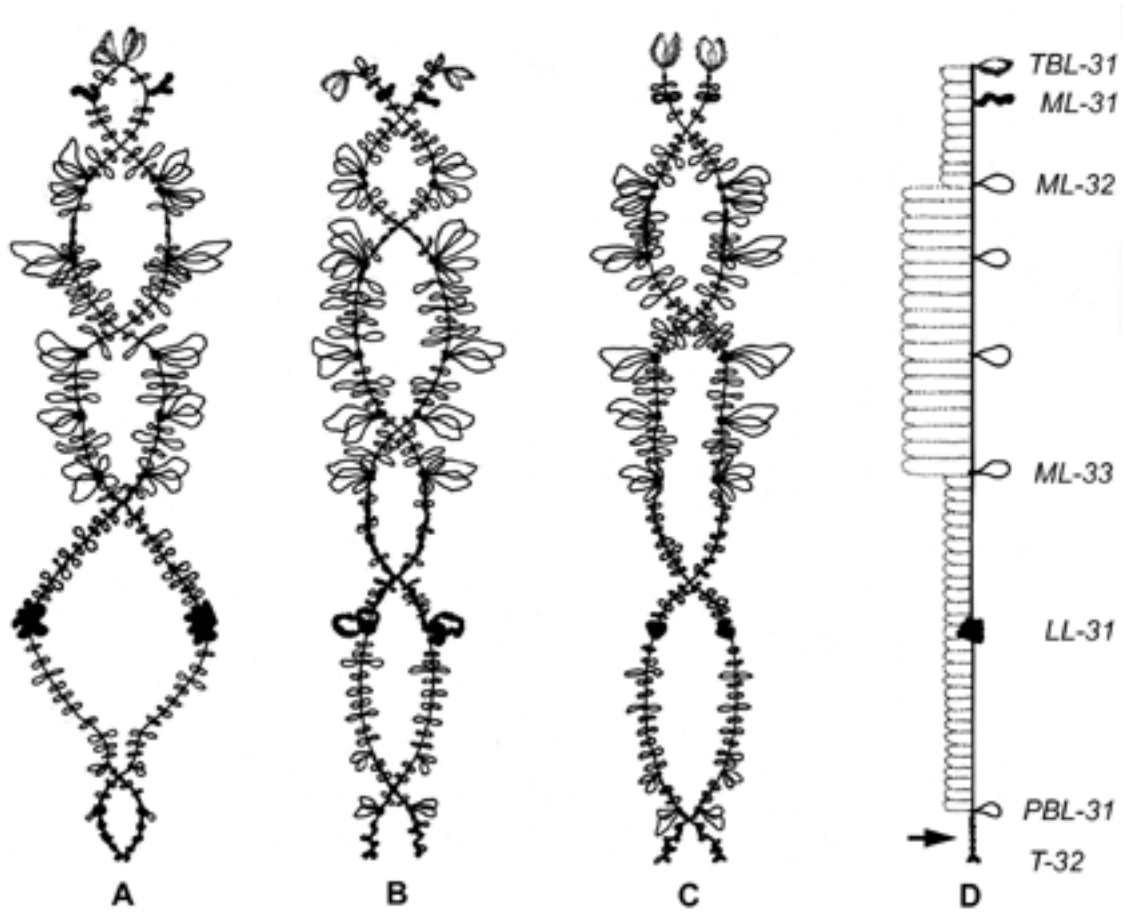

Figure 3. Schemes and a working map of the chicken lampbrush bivalent C.

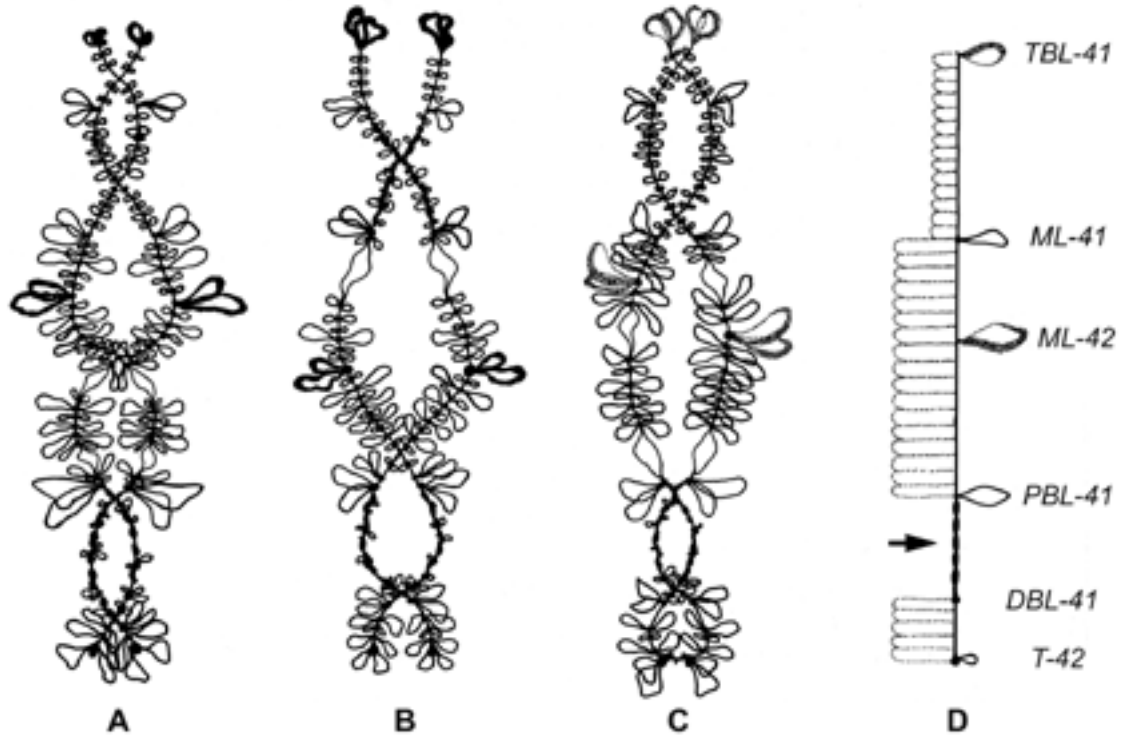

Figure 4. Schemes and a working map of the chicken lampbrush bivalent D.

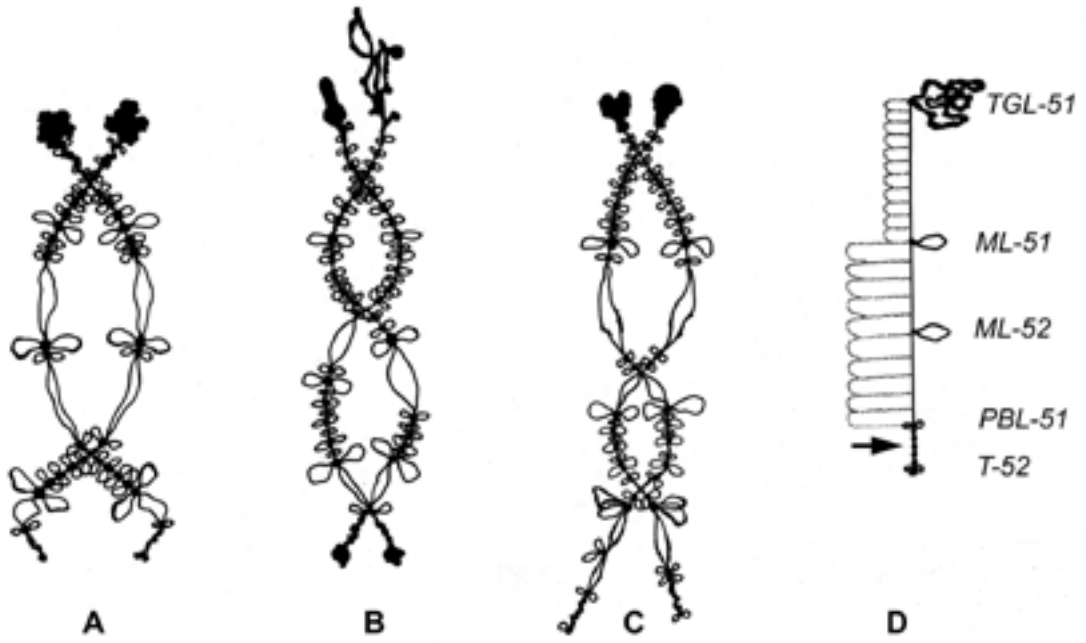

Figure 5. Schemes and a working map of the chicken lampbrush bivalent D.

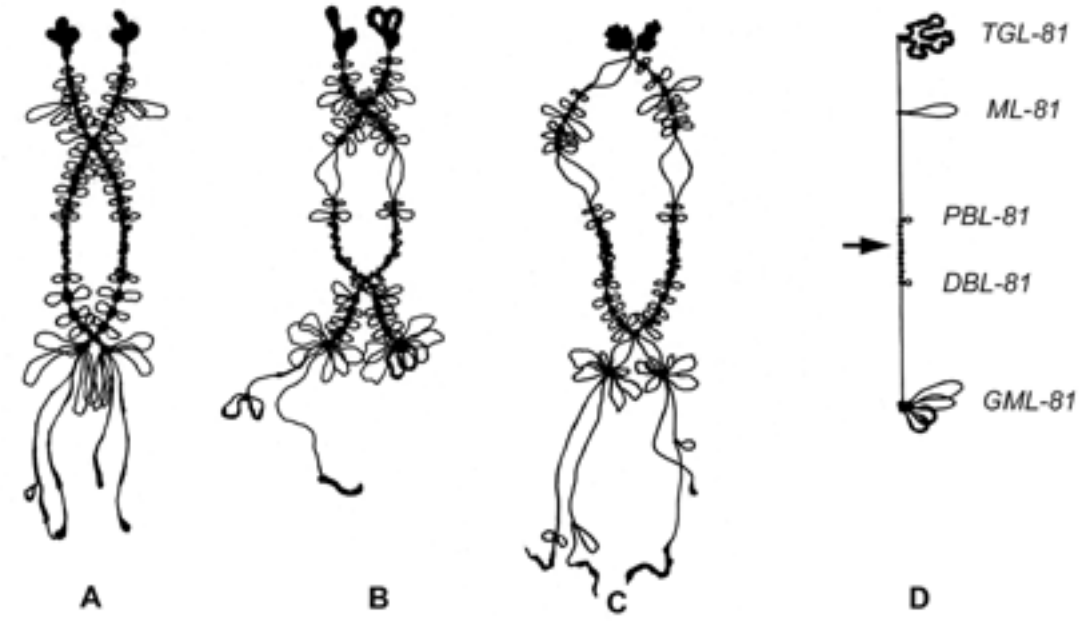

Figure 6. Schemes and a working map of the chicken lampbrush bivalent D.

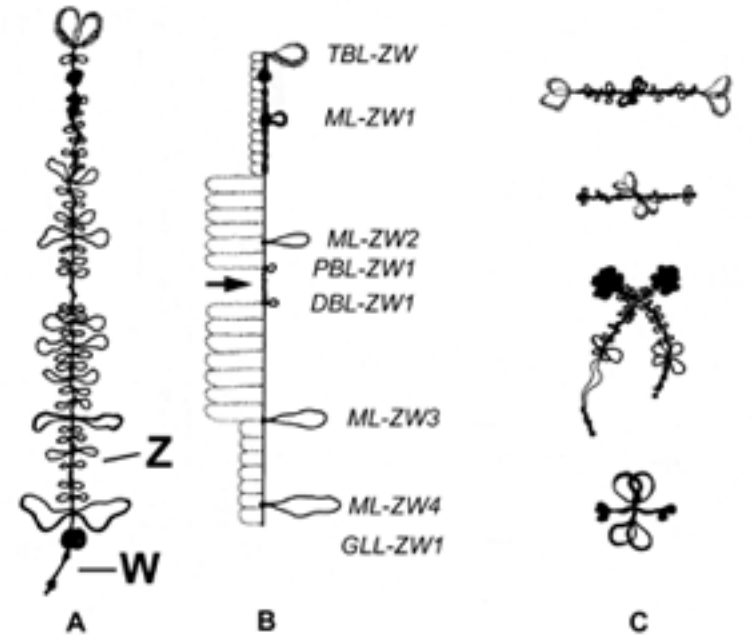

Figure 7. Scheme (a) and working map (b) of the sex bivalent ZW and the scheme of certain microchromosomes (c-e) of the chicken.

Table 1 Coordinates of Chicken Macrobivalents

Bivalent (number of studied bivalents)	Marker	Number of bivalents with the marker observed	Co-ordinates
A (25)	TBL-11	25	0
	ML-11	15	0.217+0.048
	ML-12	11	0.255+0.070
	DBL-11	15	0.378+0.063
	PBL-11	24	0.439+0.011
	ML-13	16	0.485+0.020
	ML-14	20	0.524+0.019
	PBL-12	24	0.580+0.005
	DBL-12	25	0.636+0.004
	ML-15	11	0.715+0.031
	PBL-13	19	0.893+0.029
	DBL-13	22	0.952+0.025
	T-12	25	1
B (23)	TBL-21	23	0
	LL-21	22	0.042+0.003
	DBL-21	45	0.110+0.014
	PBL-21	15	0.175+0.023
	ML-21	15	0.291+0.041
	ML-22	16	0.586+0.073
	PBL-22	22	0.602+0.016
	DBL-22	22	0.666+0.018
	ML-23	3	0.706+0.185
	ML-24	10	0.809+0.055
	LL-22	20	0.902+0.025
	T-22	23	1
C (15)	TBL-31	15	0

	ML-31	**10**	**0.026+0.007**
	ML-32	**9**	**0.168+0.046**
	ML-33	**15**	**0.579+0.084**
	LL-32	**14**	**0.746+0.016**
	PBL-31	**9**	**0.905+0.047**
	T-32	**15**	**1**
D (15)	**TBL-41**	**15**	**0**
	ML-41	**8**	**0.297+0.107**
	ML-42	**13**	**0.439+0.042**
	PBL-41	**13**	**0.674+0.025**
	DBL-41	**13**	**0.8164:0.030**
	T-42	**15**	**1**
E (10)	**TGL-51**	**10**	**0**
	ML-51	**9**	**0.307+0.038**
	ML-52	**8**	**0.495+0.029**
	PBL-51	**9**	**0.900+0.046**
	T-52	**10**	**1**
F (7)	**TGL-F1**	**7**	**0**
	PBL-F1	**7**	**0.494+0.023**
	DBL-F1	**7**	**0.719+0.019**
	GML-F1 (T-F1)	**7**	**1**
ZW (19)	**TBL-ZW**	**19**	**0**
	ML-ZW1	**13**	**0.153+0.031**
	ML-ZW2	**5**	**0.360+0.231**
	PBL-ZW1	**14**	**0.470+0.068**
	DBL-ZW1	**14**	**0.567+0.083**
	ML-ZW3	**5**	**0.786+0.360**
	ML-ZVV4	**15**	**0.945+0.094**
	GLL-ZW1	**19**	**1**

[1] The number of bivalents studied is contained in parentheses.

Table 2. Centromeric indexes, average lengths and coefficients of the decompactization of chicken chromosomes in the metaphase of mitosis and in meiosis at stages of the synaptonemal complexes and lampbrushes

Chromosome number	Chromosome parameters		
	mitotic metaphase[1]	meiotic pachitene (SC stage) [2]	meiotic diplotene (lampbrush stage) [3]
chromosome length (μ), x+:s -			
1	6.60+0.08	33	185.2±6.3
2	5.00+0.07	26	150.6±1.3 128.0±3.1 107.2±3.4
3	3.80+0.05	18	
4	3.00+0.03	15	
5	2.00+0.03	11	
6	1.50+0.02	7	
7		6	
8		6	36.5±2.1
Centromeric index			
1	39.4	39.4	39.2
2	36.0	37.0	36.6
3	A[2]	5.3	4.8
4	23.3	25.0	25.5
5	A[2]	9.1	5.0
6	A[2]	14.2	
7	—	16.7	
8	—	33.3	39.4
De-compaction index			
1	1	5.0	28.1
^	1	5.2	30.1
3	1	4.7	33.7
4	1	5.0	35.7
5	1	5.5	36.0
6	1	4.7	
7	1		
8	1	—	—

[1] According to Eramatov's data (1983)
[2] Calculated on Rahn and Solari's data (1986)
[3]0ur own data.

Relation of the length of synaptonemal complex or lampbrush to the length of the corresponding chromosome in the metaphase of mitosis.