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Avian Meiotic Chromosomes as Model Objects in Cytogenetics

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1. Introduction

The beginning of the new millennium proved critical for life sciences. The team of scientists working on the Human Genome Mapping Project published and made available on the website of *Nature* a complete set of information on the human genome. Almost simultaneously an independent private company, Celera Genomics, published the results of its study of human DNA sequence in *Science*. The dream of scientists trying to read the human genome sequence for the last ten years was fulfilled. The end of the related rivalry was the beginning of a new epoch and a new field in genetics – genomics.

At present, genomics and cytogenetics are the two fastest-developing genetic disciplines. Genome mapping and karyotype standardization projects involve an increasingly greater number of animal and plant species. Genome exploration by physical mapping requires a knowledge of the karyotype of a given species for which the map is being created. The gene/chromosome interdependence is investigated through cooperation between international mapping projects and international karyotype standardization programs. A particularly dynamic rate of progress is observed in mapping the genomes of higher vertebrates. The most numerous group of vertebrates is constituted by birds and, as a paradox, it is their genome that is least well-known. Although they guard the secrets of their karyotype with the high diploid number and microchromosomes, birds have meiotic chromosomes of easy access and the intriguing lampbrush chromosomes.

The high number of chromosomes and the presence of microchromosomes in the avian karyotype have made cytogeneticists look for other sources of information on chromosomes. The extension of cytogenetic investigations over a greater number of chromosomes required the use of chemical agents, such as amethopterin or thymidine that inhibit chromosome condensation. Such experiments were undertaken on hens and produced poorly condensed chromosomes with bands in fine resolution. This made it possible to identify sixteen chromosome pairs.

Meiotic chromosomes are a valuable object for avian karyotype analyses. Meiosis is normally observed in males, as spermatocytes are relatively small, numerous and readily available. The most often analysed meiotic chromosomes are those contained in cells in the pachytene and diplotene of the first meiotic division. The experiments have predominantly

concerned samples of testes. The observation of female meiotic chromosomes is limited by the large size of the egg cell, technical difficulty in sampling chromosomes from the egg cell and low numbers of the cells as compared with spermatocytes. Nevertheless, female meiotic chromosomes are worth paying attention to. The maturing oocytes isolated form the ovaries constitute the material for this type of experiments. Meiosis guarantees the stability of the chromosome number in the consecutive generations of sexually reproducing organisms. Generally, meiosis is represented as a process during which the cell passes through totally different stages that correspond with particular structure and behaviour of chromosomes. The observation of the changes occurring in the structure of meiotic chromosomes leads to an understanding of the nature of meiosis. The first prophase of meiosis, in which the crossing-over takes place, should be paid particular attention.

2. Lampbrush chromosomes

Oocytes – female reproductive cells are formed in oogenesis in ovaries. After the mitoses cease, the oogonia (primary sex cells) become first-order or primary oocytes. Next, they quickly enter the S phase, the preleptotene during which DNA is replicated for the last time. The oocyte grows during the meiotic prophase and, in most animals, stops expanding in the metaphase of the first meiotic division. Most of this cell growth takes place in the diplotene stage. In that stage, diplotene chromosomes of some vertebrates, e.g. birds assume the form of lampbrush chromosomes and generate thousands of loops along their axis, interpreted as sites of transcriptional activity (Macgregor & Varley, 1988; Morgan, 2002).

Lampbrush chromosomes still need to be fully explored. It is still unknown how they form out of the small mitotic structures, nor how they function in the oocyte. What is known is that they are intermediary structures present in the first meiotic division in the prolonged diplotene stage. They originate from a small telophase form at the end of the last oogonium mitosis. As they enter the diplotene stage of the first meiotic division, they undergo rapid decondensation that generates very large chromosome structures (Macgregor & Varley, 1988; Schmid et al., 2005).

Lampbrush chromosomes were discovered in 1882 by Flemming who observed salamander egg cells (*Ambystoma mexicanum*). Ten years on, LBCs were identified in shark egg cells and described by Rückert. It was Rückert who introduced the term "lampbrush chromosome" into biological nomenclature. The chromosomes take their name from 19th century brushes for cleaning street lamps to which Rückert likened them. The modern version of the item are bottle or test-tube brushes (Fig. 1) (Callan, 1986; Macgregor, 1977, 1980, 1987; Macgregor & Varley, 1988).

Lampbrush chromosomes are intermediate structures present during the first meiotic division. In the prolonged diplotene stage, they undergo decondensation that produces very large chromosomal structures. LBC length ranges (depending on the species) from 400 to 800 μm, which makes them up to 30 times larger than their mitotic counterparts (Callan, 1986; Callan et al., 1987; Rodionov, 1996). The basic profile of LBCs is performed with a 20x zoom of the microscope. In the case of avian mitotic chromosomes, a 20x zoom only makes it possible to identify the metaphase plate, not always enabling the determination of the number of chromosomes.

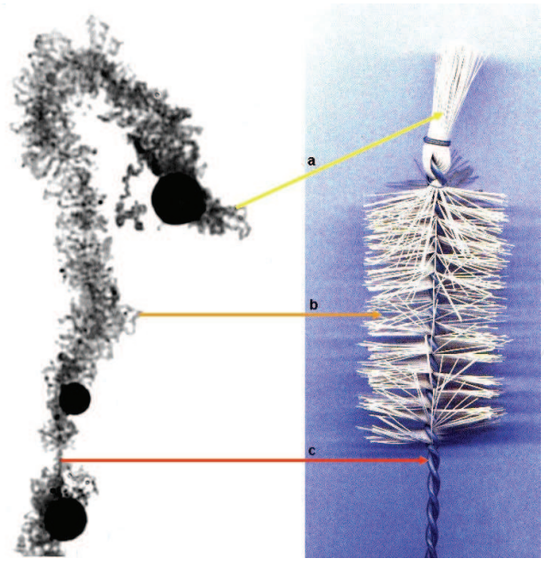

Fig. 1. A lampbrush chromosome and the "original item". The arrows indicate analogous structures; a- telomeric loop, b- side loops, c- a chromatid without loops (Katarzyna Andraszek).

Figure 2 shows a 20-fold microscopic magnification of the metaphase plate (a) compared in size with (b) 100-fold magnification of the second-pair mitotic chromosome) a 20-fold magnification of the second lampbrush bivalent (c). The arrow shows the second-pair mitotic chromosome on the metaphase plate.

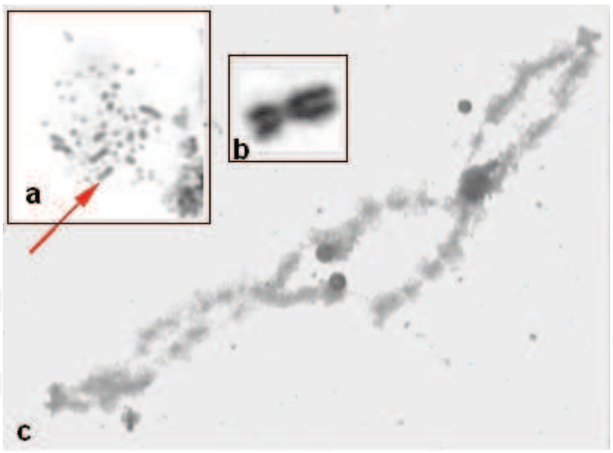

Fig. 2. A comparison of the size of LBC and mitotic chromosomes (Katarzyna Andraszek).

In the early prophase, a lampbrush chromosome is a bivalent that consists of two conjugating homologues ultimately becoming a tetrad. The axis of each of the homologue chromosomes is constituted by sister chromatids. Each chromatid is composed of alternately positioned regions of condensed inactive chromatin (chromomeres visible as dark irregular structures and also observed in the interphase nucleus) and side loops of decondensed chromatin. In the homologous sections of the bivalent, chromatin is condensed (spirally twisted) or decondensed in the form of side loops – two per each chromosome and four at

the level of the bivalent. The loop constitutes a part of the chromosome axis. It is both extensible and contractible. The contractibility of the loop results in the contraction and dilation of the chromomere (Angelier et al., 1984, 1990, 1996; Chelysheva et al., 1990; Macgregor, 1987; Morgan, 2002).

The use of a 100x zoom to analyse LBC structure made it possible to observe chromomeres, chiasmata and sister chromatids of each bivalent homologue. The identical zoom used for the analysis of avian mitotic chromosomes enables only the identification of their morphological structure in relation to the first couple of macrochromosome pairs. Figure 3 shows a 20-fold magnification of the second goose bivalent (a) and its distinctive structures visible with a 100x zoom (b, f – telomeres, c – centromere, d – chiasm, e - sister chromatids). In the case of the structural analysis of male meiotic chromosomes it is not possible to observe these crucial meiotic cytogenetic features.

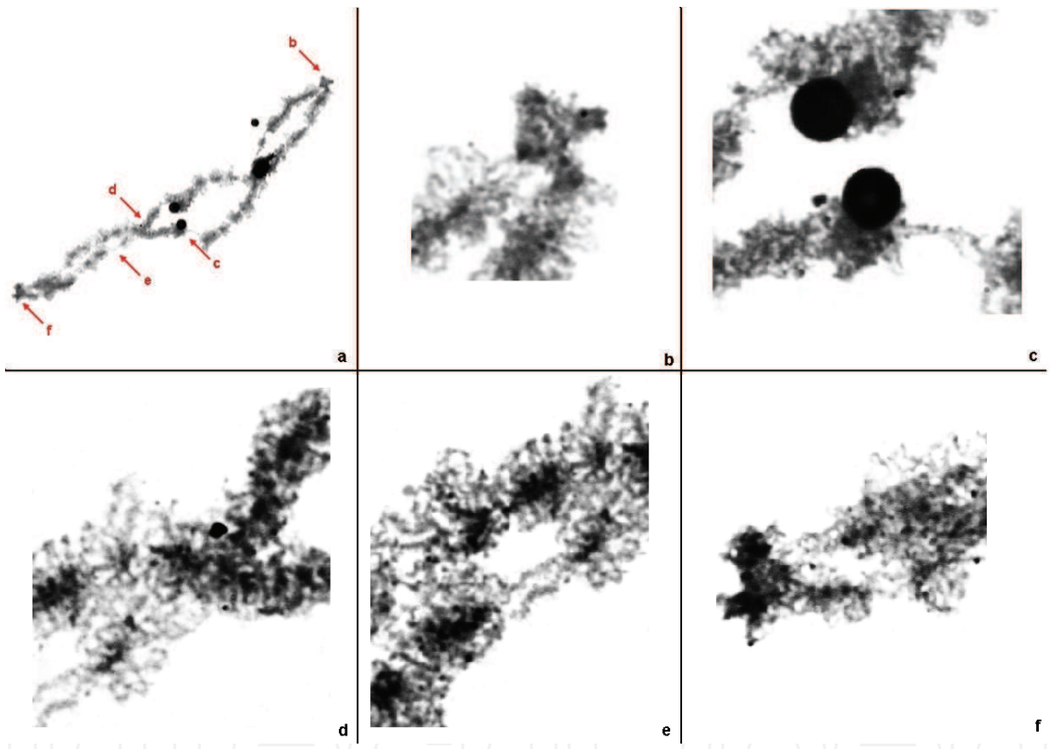

Fig. 3. The second goose LBC with a magnification of its distinctive structures (Katarzyna Andraszek).

As a tool, lampbrush chromosomes were introduced into poultry cytogenetics by Kropotova and Gaginskaya (1984), and by Hutchison (1987). The former authors support a thesis that chromosomes provide valuable information on bird gene expression, and are irreplaceable in cytogenetic research on animals with small genomes in which a large number of small-sized mitotic chromosomes makes it impossible for scientists to carry out microchromosome analysis. Just like in the case of banded patterns of mitotic chromosomes, LBCs are characterised by a special arrangement of active and inactive chromomeres visible as a pattern of side loops and regions without loops. In the Second Report on Chicken Genes and Chromosomes LBCs have been recognised as a new model in avian cytogenetics (Schmid et al., 2005).

Lampbrush chromosomes represent a new model in avian cytogenetics and are increasingly more often used in poultry chromosome analyses. Additionally, lampbrush chromosomes are considered as model structures in the study of transcription regulation. Changes in transcription activity are reflected as modifications of LBC morphological structure and are associated with physiological processes of the organism. The transcription activity analysis is carried out according to the concept assuming that it takes place in LBC side loops.

The aim of the present study (Andraszek et al., 2009; Andraszek & Smalec, 2011) was to compare the structure of the first five lampbrush macrochromosomes and ZW sex lampbrush bivalents, sampled from the oocytes of geese prior to and after the reproductive period and compare the transcription activity of lampbrush chromosomes and the G band pattern of corresponding mitotic chromosomes of the European domestic goose Anser anser.

The pre-reproduction bivalents were marked with lowercase "a", the post-reproduction ones with lowercase "b". The marker structures of the bivalents were successively numbered. The structure of the lampbrush chromosomes was analysed paying special attention to the comparison of the transcription-active parts and the GTG pattern on the corresponding mitotic chromosomes. The following marker structures were identified in the LBCs under analysis: GLLs – giant lumpy loops, MLs – marker loops, DBLs – distal boundary loops, PBLs – proximal boundary loops, TLs – telomeric loops, TBLs – telomeric bow-like loops, TLLs - telomeric lumpy loops, DBs – double bridges, Chs – chiasmata, PBs – protein bodies.

The respective bivalents sampled prior to and after reproduction have similar sizes but differ in morphological structure. The lampbrush chromosomes sampled after reproduction have reduced side loops – sites of intensive transcription activity. On the other hand, inactive chromomeres become prominent in the chromosomes. Marker loops are those structures that are degraded last after the end of reproduction. Consequently, they are used as the basis for identifying particular bivalents at different stages of transcriptional activity of the cell. The dark blocks correspond to the location of transcription active regions.

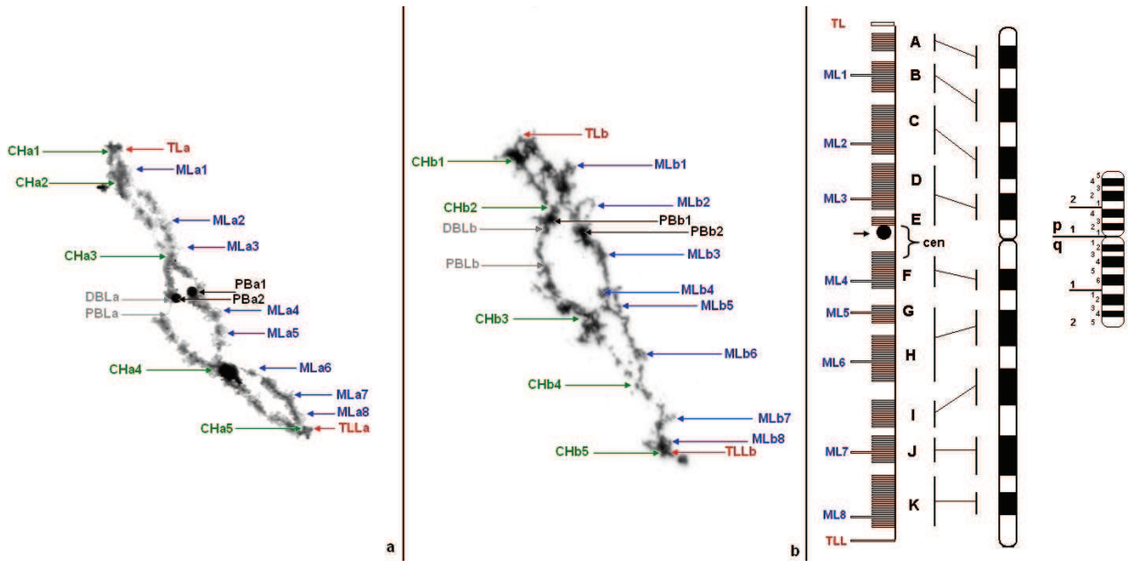

Fig. 4. Comparison of the structure of LBC 2 prior to (a), after (b) the reproductive period and graphic comparison of transcription activity of the second LBC and G bands on the second mitotic chromosome (c). Arrows indicate marker structures of bivalents.

The comparison of the location of regions with and without loops of the analysed lampbrush chromosomes with the GTG pattern of the corresponding mitotic chromosomes revealed that the arrangement of regions with side loops on LBCs which are transcription active corresponded to the GTG pattern on the mitotic chromosomes.

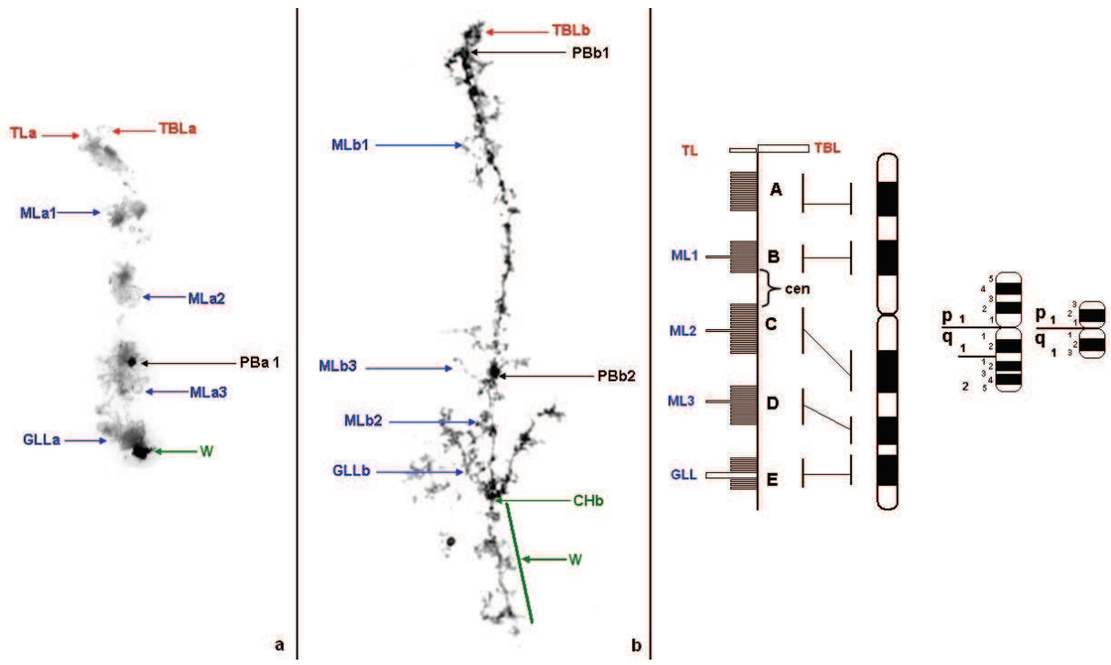

Fig. 5. Comparison of the structure of sex LBC prior to (a), after (b) the reproductive period and graphic comparison of transcription activity of the sex LBC and G bands on the sex mitotic chromosome (c). Arrows indicate marker structures of bivalents.

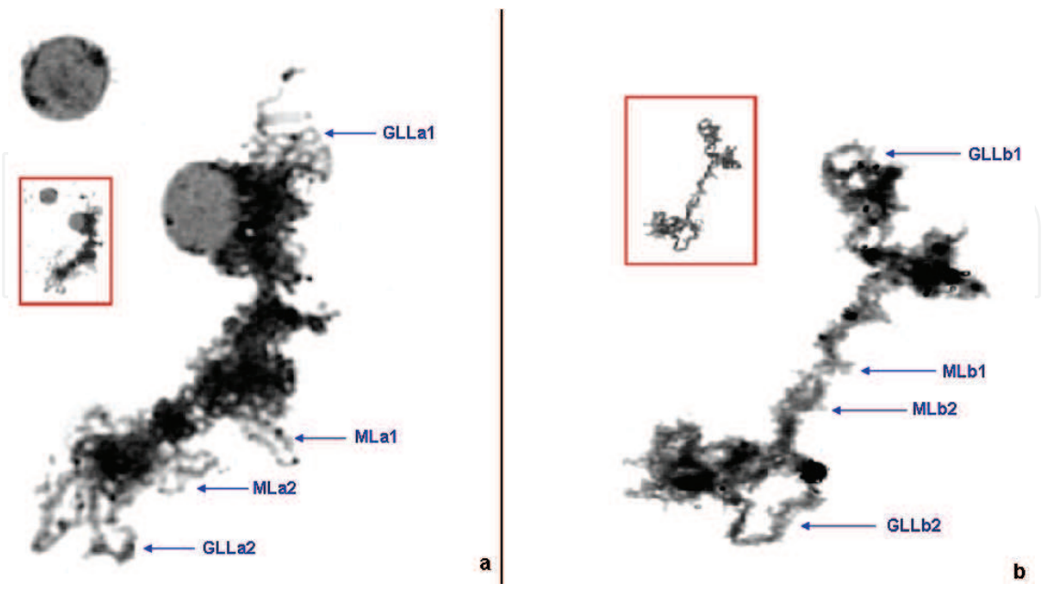

Fig. 6. Comparison of the structure of the micro-LBC prior to (a) and after (b) the reproductive period. Arrows indicate marker structures of bivalents.

Particular interest in recent years has been devoted to possibilities of using lampbrush chromosomes in genome mapping. This strategy can combine chromosome marker mapping and physical gene mapping using the in situ hybridisation technique with genetic maps constructed on the basis of chiasm incidence in the analysed bivalents. Equally important is also the possibility of using lampbrush chromosomes in analyses of the interaction of genes with other cellular structures. Particularly promising seem to be the possibilities of using lampbrush chromosomes in the mapping of avian genomes. This strategy can combine chromosome marker mapping and physical gene mapping using the FISH technique with genetic maps constructed on the basis of chiasm incidence in the analysed bivalents.

3. Meiosis during spermatogenesis

The cytogenetic analysis of breeding animals is problematic in the case of birds. The reason for the stalemate in research are the specific characteristics of the avian karyotype. A typical avian karyotype consists of several or a dozen or so macrochromosomes and about sixty microchromosomes. (Christidis, 1989; 1990). The only systematic description of avian chromosomes is the karyotype of the domestic hen (Smith et al., 2000).

A high number of chromosomes and the presence of microchromosomes in the bird karyotype made cytogeneticists look for other sources of information on the chromosomes. An important material for the analysis of the avian karyotype are meiotic chromosomes. The earliest studies of meiotic chromosome structure were conducted in the United States. The first investigations provided information on the huge variability of meiotic chromosomes, even within one genus. Among Batrachoseps salamanders, some species were unique in having a specific stage of chromosome dispersal between pachytene and diplotene, whereas no such phase was observed in other species (Macgregor & Varley, 1988).

Meiosis is usually observed in males, as spermatocytes are relatively small, numerous and easily accessible. The observation of meiotic chromosomes in females is impeded by the large size of the egg cell, technical difficulty in acquiring chromosomes from the egg cell and the fact that, compared with spermatocytes, oocytes are so few. Meiotic chromosomes are most often analysed in pachytene and diplotene cells during the first meiotic division. Cells typical of the 2nd meiotic division are few. Therefore, colchicine and vinblastine sulphate are applied to increase the number of the cells (Fechheimer, 1990).

In contrast to mitotic chromosome analyses, the number of studies of avian meiotic chromosomes is limited. Miller was the first to analyse meiosis in Gallus domesticus in 1938. He used primary spermatocytes of cocks as the experimental material. He identified 39 or 40 bivalents in metaphase I (Ford & Woollam, 1964). Similar experiments were performed by Ohno (1961). He identified 39 bivalents in Gallus. Moreover, he concluded that micro- and macrochromosomes follow identical behaviour during meiosis. The abovementioned studies concerned only diakinesis and the pre-meiotic phase and were conducted on a small number of cells sampled from several animals. Comprehensive information on meiotic chromosomes and the process of meiosis in hens was provided by Pollock & Fechheimer (1978). They analysed chromosomes at every stage of meiosis. Additionally, the number of chiasmata in the bivalents was determined. A separate group of studies of meiotic chromosomes in Gallus is constituted by analyses of synaptonemal complex structure both

in spermatocytes (Kaelbing and Fechheimer, 1983, 1985) and oocytes (Solari, 1977; Rahn & Solari, 1986; Solari et al., 1988).

A paper by Andraszek and Smalec (2008) presents the course of meiosis in goose spermatocytes, with particular emphasis on the first meiotic prophase, the stage at which crossing over takes place, a process that guarantees recombination variability of organisms.

The results provided in the publication represent the only available study of avian meiosis in the relevant literature. They can be treated not only as practical reference data on the cytogenetics and biology of bird reproduction but also as didactic material.

Figure 7a shows the early prophase of the first meiotic division - leptotene. At this stage, chromosomes have the form of thin and long chromatin threads within which the chromatids cannot be distinguished. It is impossible to distinguish particular chromosomes which resemble an entangled wool-ball. In Figure 7b, early prophase chromosomes are also visible. Gradual chromatin condensation that occurs during the entire prophase causes the chromosome looping to become looser offering the possibility to distinguish particular chromatin threads. At this stage it is still impossible to distinguish particular chromosomes.

Figure 7c shows an image of late-zygotene bivalents. Due to progressive chromatin condensation particular chromosomes become separated. They are still long, while the chromatids remain indistinguishable. At this stage in the prophase, it is already possible to discern macro- and microchromosomes. However, it still remains impossible to identify particular homologous chromosomes, as they conjugate over their entire length. At this stage, synaptonemal complexes are observable only with an electron microscope. Figure 7d shows late-pachytene bivalents. Due to progressive chromatin condensation, particular bivalents are already distinguishable. It is possible to discern particular bivalents. Meiosis is not a strictly synchronous process. In some cells it is still impossible to recognise the homologues of the bivalent, since they conjugate over their entire length. Arrows in Figure 7e show the initiation sites of synaptonemal complex degradation . Figure 7f shows typical early-diplotene chromosomes. The cell is preparing for crossing over. The bivalents begin to divide into chromatids. At some points in the chromosome it is possible to observe chiasmata (indicated with arrows). The next Figure 7g depicts meiotic chromosomes in early diakinesis. Arrows indicate the prominent chiasmata, discernible due to gradual chromosome condensation. At this stage, the chromosomes are already after recombination. During the entire prophase, the nucleoli disintegrate. However, they remain observable until the end of the first meiotic prophase. Different numbers of bivalent-specific nucleoli (indicated with arrows) (Figure 7h) of different sizes (figure 7i) were observed in the analysed preparations. Figure 7j shows an image of a cell in late diakinesis, after the terminalisation of chiasmata. The chromosomes, with discernible micro- and macrochromosomes, contain condensed chromatin. A cell with such organisation enters the metaphase of the first meiotic division.

The work did not attempt to profile the cells in the remaining meiotic stages. Cells that are observed during the second meiotic division are the rarest category of reproductive cells in cytogenetic analysis. Even if they are visible under the microscope, the quality of definition is not satisfactory enough to enable description. Apart from that, the authors intended to focus on the prophase of the first meiotic division, the stage at which the recombination of the genetic material occurs.

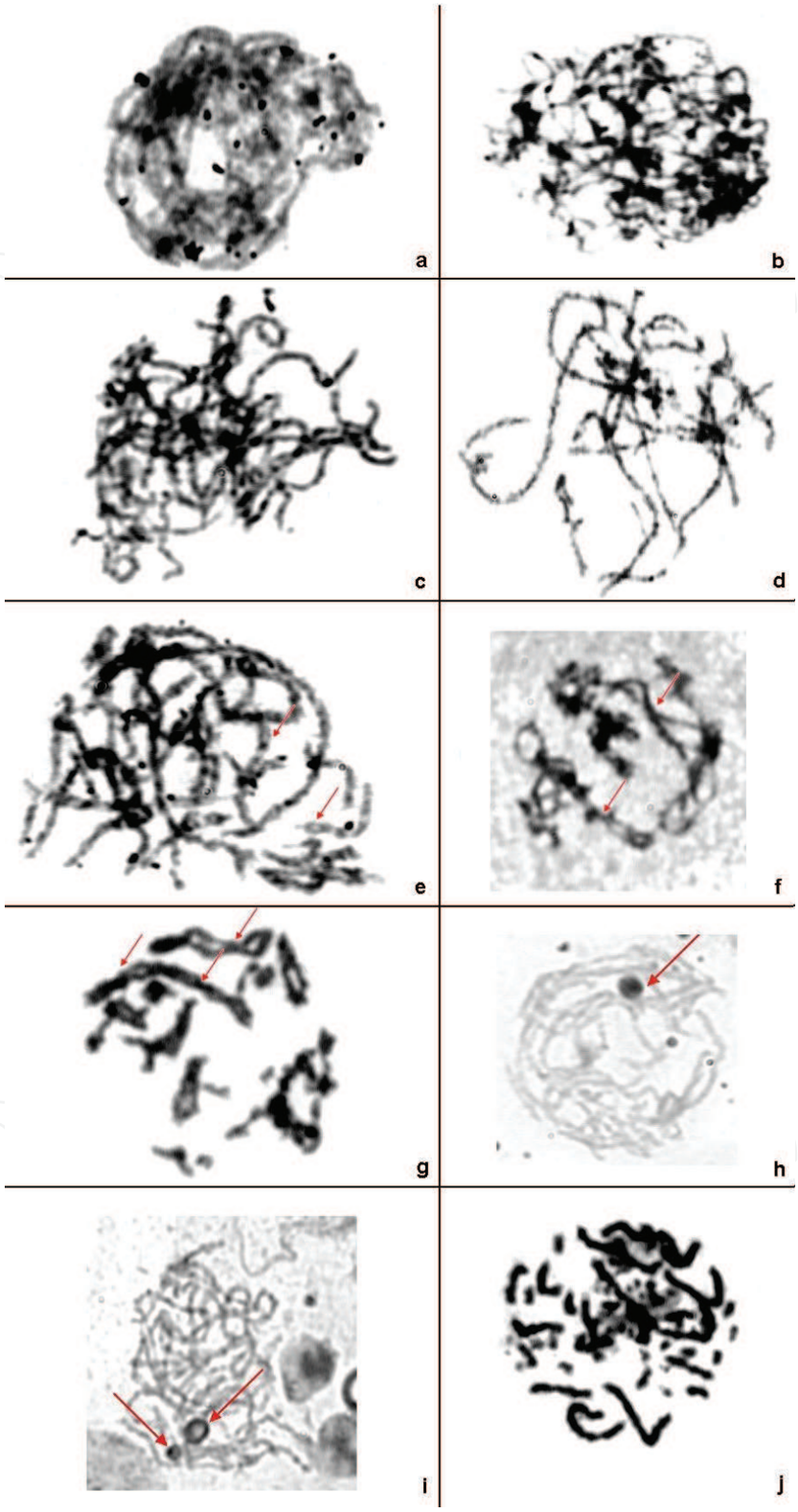

Fig. 7. The prophase of the first meiotic division in domestic goose spermatocytes.

4. Synaptonemal complex

A structure that is inextricably associated with the meiotic division of the cell is the synaptonemal complex (SC) - a proteinic structure which binds homologous chromosomes during the prophase of the 1st meiotic division and ensures correct genetic recombination. Apart form mutative variability, recombination variability is the reason for the huge diversity of organisms. Recombination occurs within the two homologous chromosomes that mutually exchange fragments of chromatids. This produces unique combinations of alleles of maternal and paternal origin in the genome. Due to crossing-over and DNA content reduction to the level of 1C, diploid organisms generate gametes, thus being able to create a new organism, different from the parental one.

An immense role in this process is played by the synaptonemal complex that "clasps" together two parallel homologous chromosomes and enables their conjugation (synapsis) (Turner et al., 2004). The synaptonemal complex was first observed more than fifty years ago in the spermatocytes of crayfish (Moses, 1956) and, subsequently, the dove, cat and man (Fawcett, 1956). The name of this unique nuclear structure was coined slightly later on. This meiotic structure is evolutively conservative in the bulk of sexually reproducing eukaryota, including the nonnucleated Protozoa, Fungi and algae, as well as vertebrates (Marec, 1996; Penkina et al., 2001)

A fully formed synaptonemal complex is situated between two prophase homologous chromosomes, binding them along their entire lengths into a pair that constitutes the bivalent. This is a three-tier proteinic structure that consists of two lateral elements (LE) and a central element (CE) located between them. Between the lateral elements there are recombination nodules (RN). They are ellipsoid, highly electron-absorbing protein complexes which are present only in euchromatinic regions of the chromosome (Holm & Rasmussen, 1980; Schmekel & Daneholt, 1998). At the centre of the complex it is possible to notice the so-called ladder structure produced by the linking of lateral elements with the central element using microfilaments (TFs) (Marec, 1996; Penkina et al., 2002).

The molecular structure of the synaptonemal complex can only be analysed using an electron or scanning microscope. An optical microscope, even with a high resolution and zoom, makes it possible to make out only the bivalent structure with clear-cut synaptic chromosomes. The available sources equate bivalent presence with the synaptonemal complex due to the fact that bivalent existence directly results from the presence of the synaptonemal complex. However, the bivalent and the synaptonemal complex are two separate structures. Figure shows prophase, meiotic chromosomes of a European domestic goose male (a), the ladder-like structure of the bivalents indicates that the synaptonemal complexes have fully developed (ringed in the photo). Alongside: a schematic structure of the synaptonemal complex (b).

The synaptonemal complex begins to form during the first meiotic prophase. At that time chromatin organisation undergoes dramatic changes. Starting with leptotene, chromatid DNA (present as chromatin loops) begins to connect to proteinic elements that constitute the matrix for emergent LEs. Homologous chromosomes have to be positioned in the distance of approx. 300nm for synapsis to occur (Marec, 1996). In zygotene, the homologues start to approach each other and connect using SC elements (Penkina et al., 2002).

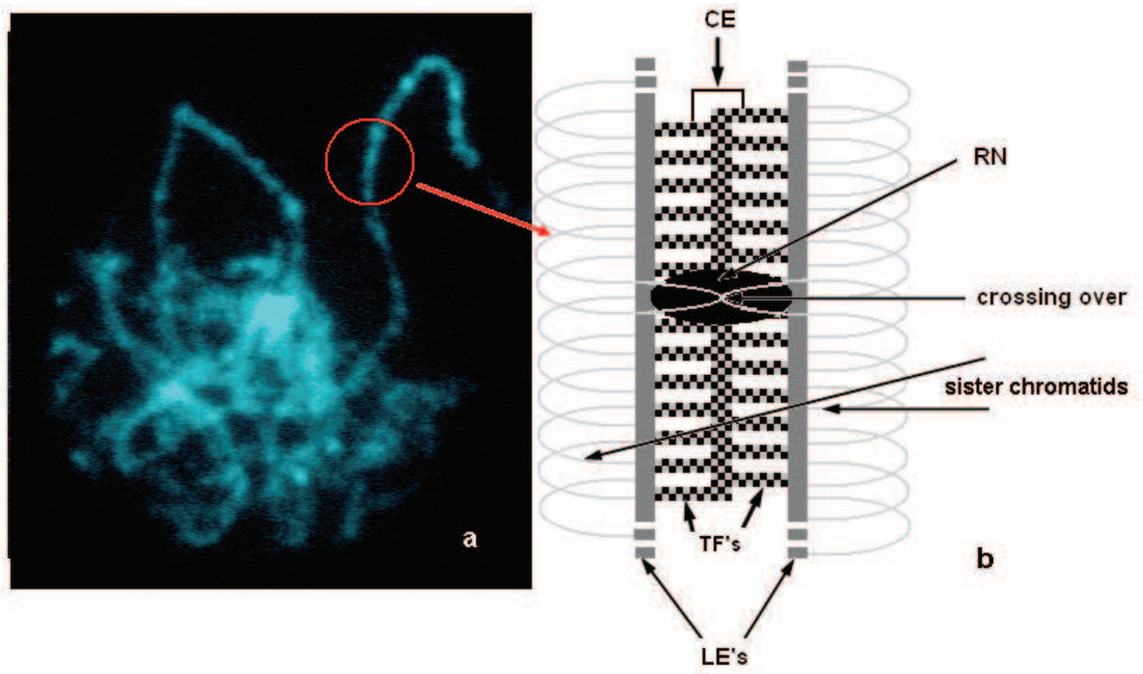

Fig. 8. The structure of the synaptonemal complex, Anser anser meiotic chromosomes, DAPI staining - (a); an outline of the synaptonemal complex – (b).

Chromatin loops depart radially from SC lateral elements. Most of the SC-bound chromatin is inactive – it is not transcribed (Marec, 1996). During the early prophase, LEs appear as proteinic axes (axial elements), each connected with two sister chromatids. Lateral elements are always built out of newly synthetised proteins, never as a result of the reorganisation of already existing components (Heyting et al., 1989). At first, LEs are visible as single, short fragments entangled in chromatin. Next, they become anchored to the inner side of the nuclear membrane with the aid of telomeres. The anchoring site of SCs is always situated in the region of the nucleus that is located opposite to the nucleolus, close to the diplosome. Lateral elements become continuous in mid-zygotene, when first complete bivalents appear and telomeres enter the distinctive bouquet stage at SC-anchoring sites of the nuclear membrane. LEs then stretch from one telomere to another in each chromosome. After LE formation, the CE begins to appear, connecting the homologues in a "zipper" fashion over their entire length, except for the sites at which the process has been inhibited by interlocking (Marec, 1996).

In early pachytene, all the homologues are in full-blown synapsis. Fragments of chromosomes that form the nucleolar organizer region are the latest to attain complete synapsis (Rasmussen, 1986; Marec, 1996). The formation of the complex in yeast and higher plants is initiated at many points in the bivalent, whereas in animals it always starts from the telomeric regions and and progresses lengthwise. Interstitial synapsis also occurs, if homologue mobility is impeded due to interengaging with other homologues – interlocking (Rasmussen, 1986; Penkina et al., 2002). SC formation is initiated in subterminal regions of the chromosome and progresses towards the nearest telomere. The above observations show that chromosome conjugation is caused by the existence of two identification sites in each

chromosome, not by absolute homology of chromosome regions. The SC retains its structure until late diplotene. The first to disintegrate are CEs. Next, LEs crack along their longitudinal axis. They are decondensed in a number of stages and the SC is removed from the bivalents (Penkina et al., 2002).

4.1 Heterochromosomal synapsis

In the cells of homogametic organisms sex chromosome pairing does not differ from autosome pairing. In species whose sex is determined by the XY or ZW pair a considerable morphological and genetic variability of these chromosomes is observed. What is problematic is the length and the gene composition of the chromosomes. In the majority of such cases chromosome behaviour during conjugation seems to be forced and slightly unnatural. Despite the abovementioned impediments, the process runs correctly, which testifies to a huge adaptative potential and dynamics of the complex (Marec, 1996; Page et al., 2006).

All of the karyologically studied birds (about 10% of the living species) have a heterogametic system of sex determination in females in the form of the ZW pair. Avian sex chromosomes are rich in euchromatin, with the exception of centromeric regions and the short arm of the W chromosome. The W chromosome is often metacentric and entirely consists of heterochromatin. During pachytene, the axes of the Z and W chromosomes form a bivalent bound by a synaptonemal complex. The length of the SC corresponds to the length of the W chromosome axis. Next, from late to mid-pachytene, the unpaired section of the Z arm shortens into a streamer-like structure so as to assume the length of fully developed SC lateral elements. In this way, the Z arm twists and forms a loop around the straight W arm. The size of this loop corresponds to the size of the non-homologous pairing region in this bivalent (Pigozzi & Solari, 1999).

The synaptonemal complex in higher organisms begins to form starting from the telomeric regions. It might seem that also in birds shorter microchromosomes would be the first to form synapsis. In preparations sampled from one-day-old Anser anser goslings it was observed that macrobivalents were the first to accomplish synapsis (Andraszek et al., 2008). Figure9a shows a cell with the developed first macrobivalent (closed arrow). The dark structures in the subproximal area of the bivalents and the dark structures on the background of chromatin are kinetochores which become intensely hued after silver nitrate staining (open arrows). Kinetochores in the subproximal regions of macrochromosomes (open arrows) evidence the submetacentric forms of the first two goose macrobivalents (Figure 9b). Figure 9c shows a cell with developed synaptonemal complexes within the first four macrobivalents and the ZW univalent, as well as within the acrocentric bivalents differing successively in size.

The phenomenon provides an explanation to the specific character of the bird genome which, unlike in mammals, possesses a marked number of telomeric sequences in the interstitial parts of chromosome arms (Solovei et al., 1994; Nanda et al., 2002). The occurrence of interstitially located telomeric sequences on macrochromosomes is connected with an increase in the number of places where the formation of SCs is initiated, which explains why synapsis is achieved quicker. Santos et al. (1993) observed that in

submetacentric bivalents synaptonemal complex formation begins from subtelomeric regions of chromosomes. In acrocentric bivalents there exist two potential initiation sites which are in the distal and proximal parts of the q arm. Short p arms pair much later.

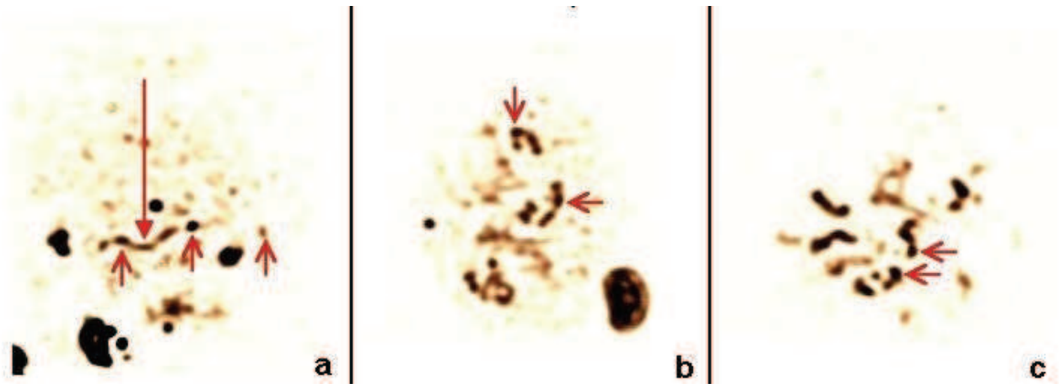

Fig. 9. Chromatin organisation in one-day-old gosling cells; isolation – Counce & Meyer (1973), staining – Howell & Black (1980)

In geese the largest macrochromosomes are submetacentric whereas the largest microchromosomes are acrocentric, so the theory of Santos et al. (1993) and the presence of interstitial telomeric sequences in chromosomes may explain why it is macrochromosomes and not microchromosomes that are the first to undergo synapsis. Moreover, compared with macrochromosomes, microchromosomes are characterised by a lower adenine-thymine content which is accompanied by a higher guanine-cytosine content (Fillon et al., 1998; Gregory, 2002). G-C-rich sequences constitute about 60% of Zyg DNA which is responsible for the linkage with SC. Zyg DNA undergoes replication not during the pre-meiotic S-phase but as late as in zygotene (Marec, 1996) so synapsis formation is delayed in those places.

It remains unexplained whether non-simultaneous synapsis is intended or coincidental, a consequence of the occurrence of interstitial telomeric sequences or Zyg DNA sequences, considering that most genes are concentrated in delayed microchromosomes (Fillon et al., 1998; Gregory, 2002). Perhaps, this is connected with the loop repair mechanism of chromosomes stuck due to interlocking. Later synapsis makes it possible for the repair mechanism to thoroughly verify whether the bivalent structure is correct, which is a way of preventing the loss of a valuable chromosome fragment. Unfortunately, this hypothesis cannot be testes as, apart from birds, no animal group has micro- and macrochromosomes in such a form.

The distinctive morphology of the ZW pair, in the form of a univalent in which chromosome W is bound to the distal part of chromosome Z, is also a consequence of synaptonemal complex formation starting from subtelomeric sequences. Moreover, as all the chromosomes start to connect and form a bivalent from telomeric sequences, the risk of losing their distal endings is reduced to a minimum. This would not be possible, if the complex formation proceeded from the centromere towards the chromosomal endings. One can think that the role of the SC is to stabilise the bivalent structure, in parallel to the role of telomeres that stabilise the chromosome structure.

The application of conventional techniques of synaptonemal complex identification and preparation staining does not make it possible to identify and analyse syn-aptonemal complex molecular structure. The presence of SCs on the preparations obtained from one-day-old goslings can be inferred from the presence of macrobivalents and darkly stained kinetochores and subtelomeric regions. In preparations obtained from 17-week-old ganders, the presence of the complexes was once again deduced from the presence of a complete set of bivalents as well as the number of kinetochores typical of the haploid set of chromosomes.

Figure 10a shows a cell with all the bivalents already visible. This is evidenced in the number of kinetochores. In the macrobivalents, kinetochores in the subproximal regions of the bivalents (open arrow) and dark-hued subtelomeric regions (closed arrow) are identifiable Figure 10b shows all the bivalents fully developed. The macrobivalents are long and well identifiable. It is possible to distinguish kinetochores and telomeric regions within them. It is also possible to observe the different lengths of the bivalents, ranging from the longest first one (closed arrow) to the very short acrocentric microbivalents (open arrow).

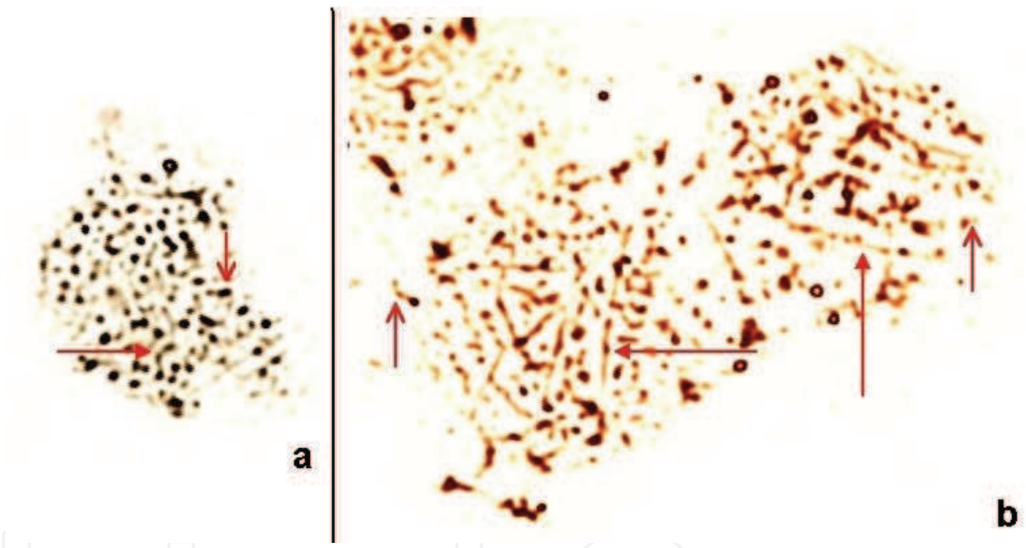

Fig. 10. Bivalent structure in 17-day-old gander cells; isolation – Counce & Meyer (1973), staining – Howell & Black (1980)

The standard technique for synaptonemal complex identification is the Counce and Meyer method (1973). The preparations for which it was used are presented above, in photograph 11a and 11b. On the other hand, promising results were obtained using the technique of meiotic chromosome isolation described by Pollock and Fehcheimer (1978), followed by silver nitrate staining and DAPI fluorochrome staining tentatively used in the experiment. After the application of the above techniques the homologues and bivalents were easily discernible. Additionally, the distinctive, ladder-like structure of synaptonemal complexes resulting from a different protein composition of the lateral elements was observed. Moreover, in the DAPI-stained preparations unique structures were identified during the basic cytogenetic analysis - two parallel homologous chromosomes just before synaptic union (Andraszek et al., 2008).

Figure 11a shows a cell with developed synaptonemal complexes within the bivalents. The structure of the complex is well visible both in the macrobivalents (closed arrow) and microbivalents (open arrow). Figure 11b shows a cell at the onset of synaptonemal complex degradation. It is possible to distinguish particular homologues of the bivalent (arrows). The distinctive synaptonemal complex structure can still be observed as alternating dark and light chromatin regions (circled) similar to the high-fidelity banding pattern of mitotic chromosomes. Such cells are typical of late pachytene and the onset of diplotene. Figure 11c shows a cell in zygotene. The homologues of the bivalents are already connected by synapsis (open arrow). In turn, the closed arrows indicate the bivalent homologues before the complete stabilisation of the SC. In Figure 11d , the bivalents have the typically synaptic ladder-like structure and prominent light fluorescent telomeres and kinetochores (open arrow) over their entire length . It is also possible to see the onset of synaptonemal complex disintegration (closed arrow) and two clear bivalent homologues after the break-up of synapsis.

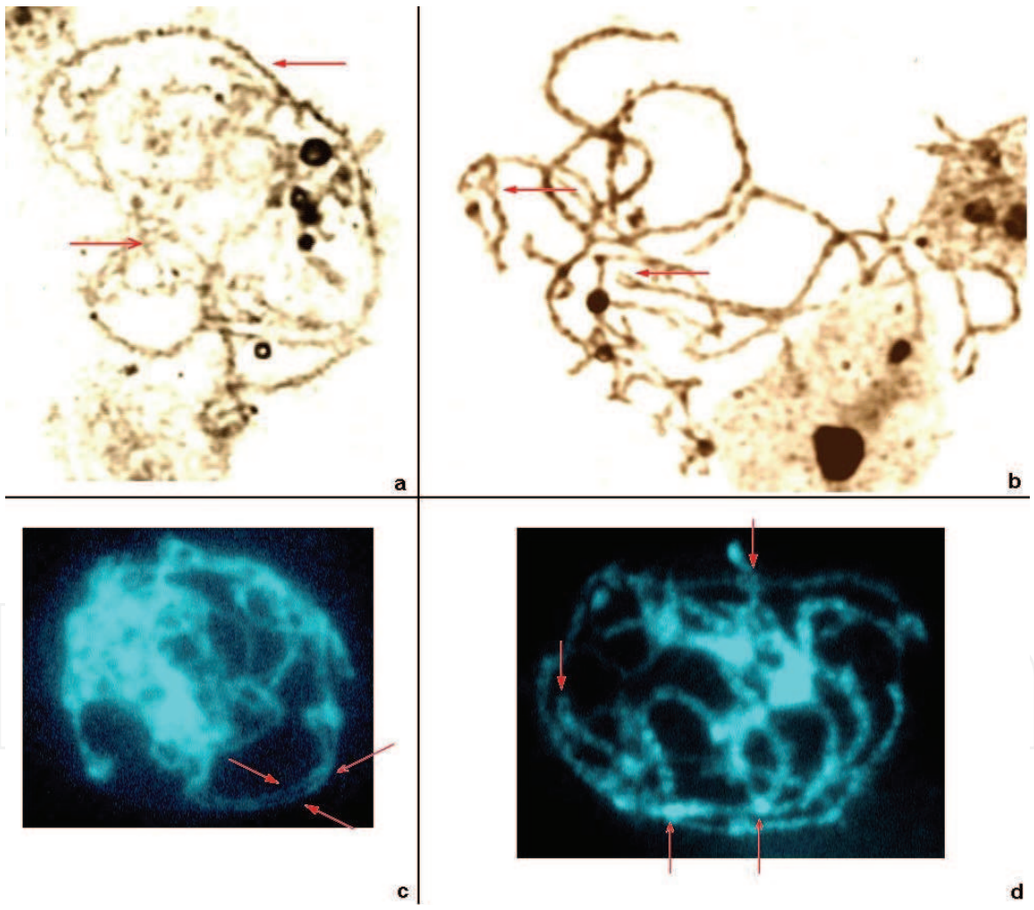

Fig. 11. Bivalent structure in 17-day-old gander cells; isolation – Pollock & Fehcheimer (1978), staining a, b – Howell & Black, c, d - Schweizer et al. (1978).

Paired or unpaired chromosome regions may indicate the chromosomal position of such marker structures as centromeres, nucleolar organizers, nucleoli, telomeres or even heterochromatin regions.

Such preparations may be very useful for analysing prophase chromosomes, and generating the so-called SC karyotypes. The karyotypes would make it possible to observe pairing initiations, sequences participating in pairing, the frequency of recombination occurrence, as well as potential meiotic chromosome structure anomalies. What follows is the fact that the complex lateral elements connect to DNA in strictly determined sequences. Thus, by convention, the ladder-like SC structure can be treated as a bivalent banding pattern indicating, similarly to banded staining, the location of specific sequences in the chromosome.

5. Nucleolus

The nucleolus is the largest and best known functional constituent of the cell nucleus. It is formed by original products of ribosomal RNA genes contained in the nucleolar organiser, related proteins and various enzymes, including RNA polymerase, RNA methylase and RNA endonuclease (Shaw & Jordan, 1995; Scheer & Hock, 1999; Hernandez-Verdun, 2006). The nucleolus is the site of synthesis and maturation of ribosomal RNA (rRNA) molecules. The molecules also bond with proteins in the nucleolus. rRNA genes are situated in particular chromosomes, in nucleolar organizer regions (NORs) that participate in the formation of nucleoli (Olson, 2004; Raška et al., 2004, 2006; Lam et al., 2005; Prieto & McStay, 2005; Derenzini et al., 2006). Nucleoli are present in the nuclei of almost all eukaryotic cells since they contain elementary metabolic genes, with the exception of spermatozoa and mature avian erythrocytes (Kłyszejko-Stefanowicz, 2002; Raška et al., 2006).

The weight of nucleoli is higher than that of the nucleoplasm in which the nucleoli are suspended. On account of its distinctive density, compact structure and low water content (10%) the nucleolus is an organelle that can be readily distinguished. Due to its characteristics, following cell nucleus fragmentation, the nucleolus remains intact in the saline solution even after the destruction of most nuclear structures, thereby allowing its isolation through centrifugation. The isolated nucleolus is identical to the one present in the nucleus of a living cell, and even retains its transcriptional activity in some cases (Olson, 2004; Hernandez-Verdun, 2006; Raška et al., 2006).

The number of nucleoli in a cell nucleus is determined by the number of active nucleolar organiser regions (NORs). It may be equal to the number of those NOR-chromosomes. Yet, normally, it is lower. This can be explained either with the fusion of nucleoli in the interphase nucleus or the suppression of activity of certain rDNA loci (Kłyszejko-Stefanowicz, 2002; Raška et al., 2006).

Nucleoli are very dynamic structures. This may be reflected in their cyclical disappearance during mitosis and reappearance at its end (Scheer & Benavente, 1990). The nucleolus disappears during cytokinesis and is reproduced in the reconstructed nuclei as a result of NOR activity (Kłyszejko-Stefanowicz, 2002; Olson, 2004) Nucleolar material appears between the chromosomes during the reconstruction of the NOR-associated telophase nucleus. Next, rRNA synthesis is resumed causing the nucleoli to become more visible. During the interphase, the nucleolus is spherical in shape. In the prophase, when the chromosomes become visible, it is evident that the nucleoli are associated with particular nucleolus organising chromosomes (Raška et al., 2006)

Both nucleoli and nucleolar organiser regions have chemical affinity for heavy metals and can be identified through staining with silver nitrate in a protective colloidal solution of formalin or gelatine (Howell & Black, 1980). Since nucleolar organiser regions (NORs) determine the structure of nucleoli, an alternative source of information on the activity of avian rRNA-encoding genes can be found in the analysis of the numbers and sizes of nucleoli in the prophase of the first meiotic division. Throughout the prophase, nucleoli are not degraded. As opposed to mitotic NORs, they are large structures (Andraszek & Smalec, 2007; Andraszek et al., 2009a; Andraszek et al., 2010a, 2010b).

The nucleoli disintegrate throughout the entire prophase of the first meiotic division. The way in which they decay is probably typical of particular vertebrate groups, this being possibly a species-specific characteristic. In the spermatocytes of domestic cattle, the nucleoli gradually become fragmented and "disintegrate" into tiny structures whose number corresponds with the number of NOR regions (Andraszek, unpublished). The studies which analysed the number and size of nucleoli in avian spermatocytes (Andraszek & Smalec, 2007; Andraszek et al., 2010b) reported a different mechanism of disappearance of nucleoli. In birds, chromatin reorganisation during the prophase of the first meiotic division and the related change in the cell nucleus size is correlated with decreasing sizes of the nucleoli. At the beginning of the prophase, in the early leptotene, the nucleoli are visible as large oval structures. In turn, at the end of the prophase they are observed as tiny points associated with specific bivalents. The figure 12 shows the different sizes of nucleoli at the beginning and end of the first meiotic prophase.

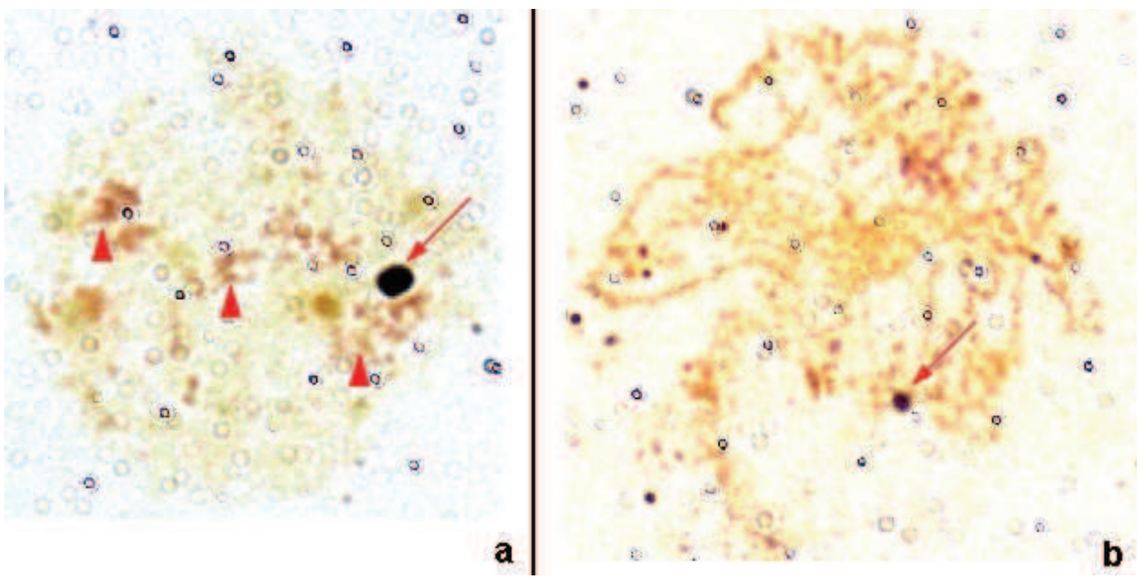

Fig. 12. Meiotic chromosomes of quail – early prophase (a), late prophase (b). The nucleoli indicated with arrows, kinetochores – arrow points.

Another distinctive characteristic of nucleoli in avian cells are the variations of their sizes unrelated with the prophase stage. Different sizes of nucleoli can be observed in cells that are at the same stage of meiosis. Figure 13 shows different sizes of nucleoli in goose (a), chicken (b) and quail spermatocytes (c).

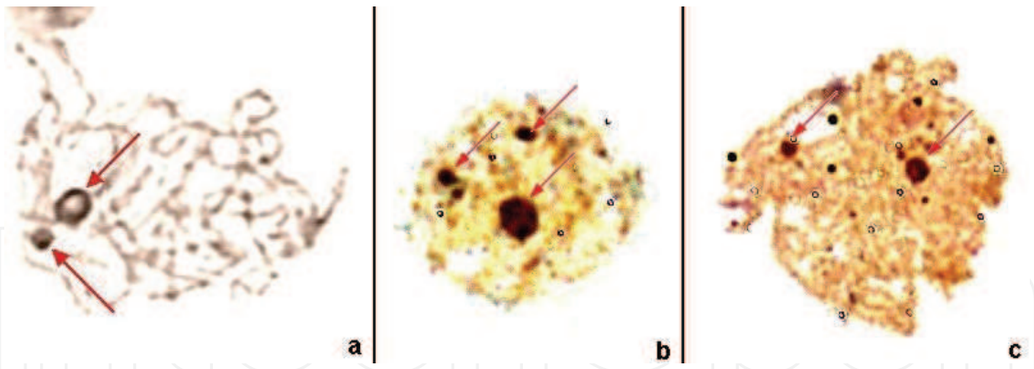

Fig. 13. Variability of the sizes of nucleoli in cells. The nucleoli indicated with arrows.

Avian cells also have variable numbers of nucleoli. This variability occurs at the individual, cellular and interindividual level. The number of nucleoli in the spermatocytes of geese and hens ranges from 1 to 4, and from 1 to 2 in quail cells. Next figures shows different numbers of nucleoli in goose (figure 14), chicken (figure 15) and quail spermatocytes (figure 16)

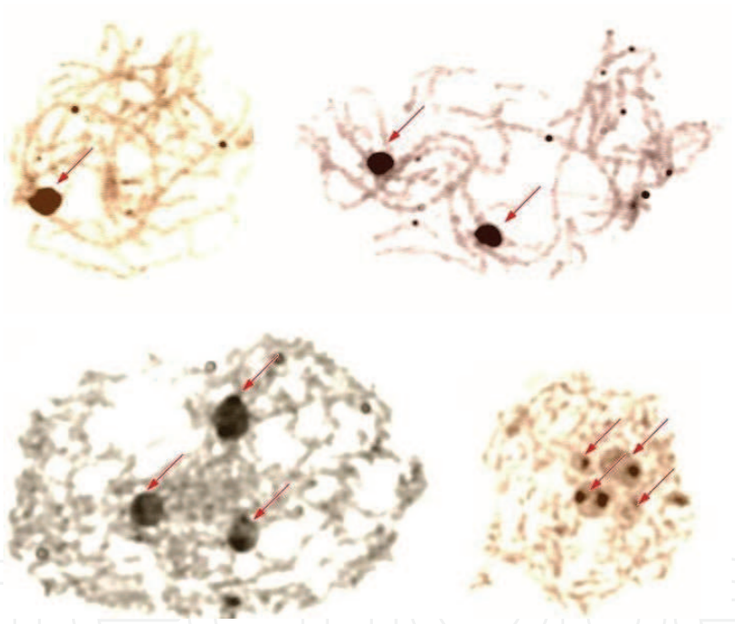

Fig. 14. Variability of the number of nucleoli in goose cells. The nucleoli indicated with arrows.

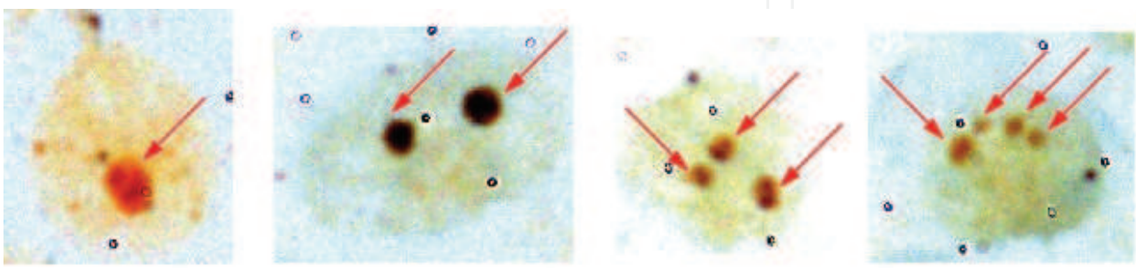

Fig. 15. Variability of the number of nucleoli in chicken cells. The nucleoli indicated with arrows.

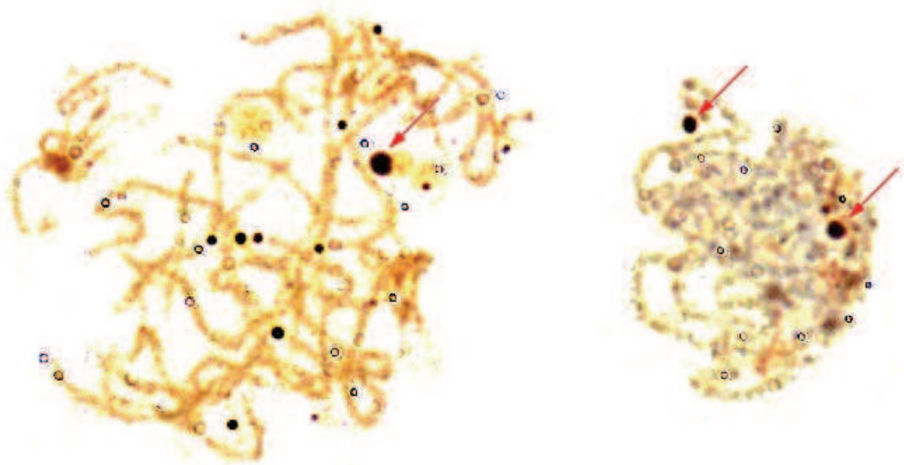

Fig. 16. Variability of the number of nucleoli in quail cells. The nucleoli indicated with arrows.

Apart from its functions being directly connected with ribosome biogenesis, the nucleolus is associated or involved in other cellular processes (Pederson, 1998; Santoro & Grummt, 2001; Olson et al., 2002; Gerbi et al., 2003; Raška et al., 2006). At present, it is not possible to determine whether these unconventional roles are the main functions of the nucleolus or adaptations of individual species or species groups. As regards the functions discussed further on, there is now a rich and still expanding body of literature available that deals with the relationship between the nucleolus and viral infections (Hiscox, 2002, 2003; Olson et al., 2002), including DNA, RNA and retroviruses.

Nucleolar morphology was one of the key criteria of neoplasm classification. The morphometric parameters of nucleoli are: the number, size and distance from the nuclear membrane (Nafe & Schlote, 2004; Smetana et al., 2005, 2006; Raška et al., 2006). Taking advantage of previous observations of Montgomery (1895), biologists dealing with neoplasms quickly tracked down the connection between AgNOR stains and cell proliferation (Derenzini et al., 1990; 2006; Raška et al., 2006).

Most studies during the last few years exploited the potential offered by the newly discovered nuclear oncogenes connected with the promotion and inhibition of tumours by cytogenetically diagnosed nucleolar mechanisms. c-Myc proteins (the product of the c-myc proto-oncogene) are located in the nucleolus and control rRNA synthesis (Oskarsson & Trumpp, 2005; Raška et al., 2006). It has also been shown that c-Myc is capable of controlling the activity of all the three polymerases in mammalian cells and coordinating the entire ribosome synthesis and cell growth (Arabi et al., 2005). These observations point at the crucial role of c-Myc in the development of promotional neoplastic actions via ribosome biogenesis control.

pRb (the protein of malignant retinoblastoma) and p53 proteins play a major role in the control of the cell cycle progress, as well as ensuring the correct development of daughter cells. These are oncosuppressive proteins, concentrated in the nucleolus (Ryan et al., 2001; Trere et al., 2004). The ARF/p16INK4a encoding gene is the second most common inactive human neoplastic gene (Ruas & Peters, 1998). ARF is situated at the nucleolus where it is

associated with p53 (Kashuba et al., 2003). It has also been observed that there is a direct functional link between the nucleolus and p53 control (Ryan et al., 2001; Olson 2004). Most stress treatments activating p53 also cause the breakdown of nucleolar structure.

A considerable number of somatic cells do not have active telomerase. This puts a limit to the number of cell division cycles and suggests that telomerase is a factor in the processes of aging and carcinogenesis (Maser & DePinho, 2002; Raška et al., 2006). Telomerase has been found to be present in the nucleolus. Its function is connected with nucleolus activity control (Raška et al., 2006). Together with a class of snoRNA, telomerase locates RNA telomerase within the nucleolus (Lukowiak et al., 2001). hTERT – the reverse transcriptase of the catalytic subunit of human telomerase also has a nucleolar location (Khurts et al., 2004). Evidence of a functional relationship between telomerase and nucleoli has been provided by studies of human cell lines (Wong et al., 2002). In tumours and transmuted cell lines hTERT was eliminated from the nucleolus (Wong et al., 2002). The nucleolar phosphoproteinic nucleoid reacts with hTERT, the interaction being affected by RNA telomerase. This interaction is probably connected with dynamic telomerase anchoring. The TRF2 binding agent of the telomere is located in certain nucleolar modifications during the cell cycle (Khurts, 2004; Raška et al., 2006).

6. Conclusion

Meiosis guarantees the stability of the chromosome number in the consecutive generations of sexually reproducing organisms. Generally, meiosis is represented as a process during which the cell passes through totally different stages that correspond with particular structure and behaviour of chromosomes. The observation of the changes occurring in the structure of meiotic chromosomes leads to an understanding of the nature of meiosis. The first prophase of meiosis, in which the crossing-over takes place, should be paid particular attention. Moreover, meiotic chromosome research makes it possible to analyse the structure of nucleoli. In the meiotic prophase, they can be an alternative source of information on the activity of rRNA-encoding genes. In addition, synaptonemal complexes, which are extraordinary structures that guarantee recombination variability of organisms, are formed during meiosis. Summing up, meiotic chromosomes can not only be successfully used in applications in reproductive cytogenetics and biology but also as didactic aids.

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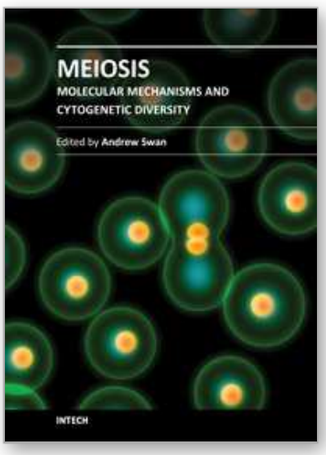

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Meiosis, the process of forming gametes in preparation for sexual reproduction, has long been a focus of intense study. Meiosis has been studied at the cytological, genetic, molecular and cellular levels. Studies in model systems have revealed common underlying mechanisms while in parallel, studies in diverse organisms have revealed the incredible variation in meiotic mechanisms. This book brings together many of the diverse strands of investigation into this fascinating and challenging field of biology.

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