Multiple synaptonemal complexes (polycomplexes) in wild-type hermaphroditic *Caenorhabditis elegans* and their absence in males

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Summary. Synaptonemal complexes are highly conserved in structure and function throughout evolution. Aggregates of these structures form a superstructure known as a Multiple Synaptonemal Complex or Polycomplex (PC). They have been described in over 70 organisms throughout all life forms including nematodes. During the stages of leptotene and zygotene, chromatin-like material, known as Extranuclear Fibrillar Material (FM), has an affinity for the nuclear envelope (NE). The FM appears inside the NE at pachytene and is closely associated with the telomeres and axial cores of the SCs. The existence of PCs in XX Wild-type hermaphrodites of *Caenorhabditis elegans*, as well as other organisms, are restricted to meiotic and germ-line derived tissues. Although PCs may be present prior to or after SC formation in other nematodes, *e.g.*, *Ascaris*, their formation and function are different at each stage. In *C. elegans*, PCs were observed only prior to pachytene, at the leptotene/zygotene interface, and disappeared afterwards. The structure and biochemical composition of PCs is similar to SCs such that the basic unit is tripartite, consisting of two lateral elements and a central region, within which transverse elements exist. The SYP-1 protein, localised in the central element of SCS in *C. elegans*, along with HTP-1 and HAL-2, are integral to the highly organised structure of the PCs. PCs were not observed in the XO male of *C. elegans*, inferring different levels of control of the pairing of homologous chromosomes and attachment to the nuclear envelope during meiotic prophase.

Key words: Synaptonemal complex, Polycomplexes, *Caenorhabditis elegans*, nematode, meiosis, pachytene.

In *C. elegans*, six synaptonemal complexes (SC) per germline nuclei were first observed in the wild-type hermaphrodite and five in the wild-type male by 3-D reconstruction analysis of serial sections from electron microscopy (Goldstein & Slaton, 1982; Goldstein, 1982). In the XX hermaphrodite, these SCs correspond to the five autosomal bivalents and the XX bivalent, while in the XO male, they correspond to the five autosomal bivalents with the X univalent lacking an SC and remaining heterochromatic throughout pachytene (Goldstein, 1987). The SC is a tripartite proteinaceous structure present between homologously paired chromosomes from yeast to humans (for review in *C. elegans* see Colaiacovo, 2006; for general review see von Wettstein *et al*., 1984).

The cooperative and progressive nature of SC assembly and the inherent tendency for self-assembly of its proteins create a situation in *C. elegans*, whereby the gametocytes must accumulate large pools of protein precursors for the central element and lateral element components of the SC. At the same time they have to prevent these precursors from aggregating into nonfunctional PCs and or interfering with the pairing of the homologous chromosomes (Zhang *et al.,* 2012). The natural proclivity of SC components for self-assembly, regardless of DNA homology, seems to be controlled by proteins HTP-1 and HAL-2 from *C. elegans*, as a key component of the mechanism preventing the stabilisation of nonhomologous contacts between chromosomes before homologue realignment has been attained (Couteau & Zetka, 2005; Zhang *et al*., 2012). Such HTP-1 aggregates, which may appear as polycomplexes (PCs), are observed in leptotene/zygotene nuclei followed by extensive localisation along unsynapsed

chromosomes. Four interdependent SYP proteins form the central region of the synaptonemal complex (SC) bridging the axes of paired meiotic chromosomes in *C. elegans* (Schild-Prufert *et al.*, 2011). These proteins provide the conserved structure and width of the SC, which is approximately 100 nm (Goldstein, 1982). The four SYP proteins are first observed as small loci on chromosomes at the transition zone in the gonad between leptotene and zygotene stages of meiosis. By pachytene, these proteins localise between the homologously paired chromosomes (Smolikov *et al.*, 2007). They are functional homologues of Zip1, which is in the central region in yeasts, and SCP1 in mammals, which can also form aggregates corresponding to higher-order structures referred to as PCses (Sym & Roeder, 1995). The mammalian SYP1 molecules localised in SCs and PCs, are highly organised within the PCs and oriented in the same manner as is SCs (Ollinger *et al*., 2005).

Multiple Synaptonemal Complexes, or PCs, were first described in meiocytes of *Blaptica dubia* (Orthoptera) (Sotelo and Trujillo-Cenoz, 1960). Such structures had a similar morphology to synaptonemal complexes (von Wettstein *et al.*, 1984); however, they differed in that they were post-pachytene and not associated with chromatin. As an isolated incident, the occurrence of PCs after meiotic prophase could be understood as an aberration during synthesis *via* increased quantity of specific meiotic proteins or in a constitutive mutant. Alternatively, they could be explained as an unusual association of dispersed SC fragments from the homologous chromosomes. However, PCs have been observed in numerous organisms, both prior to pachytene, *e.g*., *Meloidogyne* (Goldstein & Triantaphyllou, 1978) and afterwards, *e.g*., *Ascaris lumbricoides* (Fiil *et al.*, 1977) and *A. megalocephala* (Merlin *et al*., 2003). Thus, a structure conserved though evolution, such as the PC, has a specific function(s) that still is being determined.

Since PCs are associated with SCs, they may share a common developmental pathway. Examination of the origin and fate of the SC (Westergaard & von Wettstein, 1972; Gillies, 1984; Schild-Prufert *et al*., 2011) has implicated an association between PCs and SCs. For example, SC fragments retained in the chiasma region at metaphase (Holm and Rasmussen, 1983) may reorganise into PCs, thus supporting the suggestion that the PC was the last stage of SC morphogenesis (Horesh *et al*., 1979). Altered post-pachytene morphology may be the result of secondary association of its subunits (Roth, 1966). The other aspect of PC and SC morphogenesis relates to the origin of proteins in the SC.

In *C. elegans*, fibrillar material (FM), which is a precursor to PC and SC formation, is present in early meiotic prophase, *i.e*., leptotene and zygotene nuclei, and is almost identical to that previously described in *Ascaris* (Fiil *et al.*, 1977). Fibrillar material is associated with the SC in other organisms, *e.g.*, *Drosophila* (Rasmussen, 1975), such that pre-meiotic, extracellular FM was reorganized into PCs that were incorporated into nuclear SCs (Bogdanov, 1977; Fiil *et al.*, 1977). Fibrillar material may also play a role in pairing of homologous chromosomes and attachment of the telomeres to the nuclear envelope (Fiil *et al.*, 1977; Merlin *et al.*, 2003).

In this study, which examines the hermaphroditic form of *C. elegans*, PCs formed from FM prior to pachytene and this may be considered as a primary step in the development of the SC. Fibrillar material and PCs were absent in the male reproductive form, which is significant because the expression of genes on the X chromosome in the male is under a different set of regulators, known as "Disjunction Regulator Regions" (DRR) (Goldstein, 1985).

MATERIALS AND METHODS

Techniques for electron microscopy have been previously described (Goldstein & Slaton, 1982). The N2 Wild-type worms were supplied by the *Caenorhabditis* Genetics Center. For this study, 100 nuclei were examined from five different worms from each of hermaphrodites and males, throughout all stages of meiotic prophase, i.e. leptotene, zygotene, pachytene, diplotene and diakinesis. The nuclei were serially sectioned with each nucleus comprised of approximately 45-50 sections, giving an average nuclear volume of 12 μm^3. The inherent nature of the telogonic gonad in *C. elegans* provided meiotic stages that were precisely delineated by the location of the gametocyte along the central rachis (Goldstein, 1982). Distribution of fibrillar material and PCs outside and inside the nucleus, along with correlation of association with membranes and organelles, were noted.

RESULTS

Oocyte nuclei, at the stages of leptotene, zygotene and pachytene, were arranged peripherally around a central rachis of the telogonic gonad in *C. elegans* (see Fig. 1 in Goldstein and Slaton, 1982). Within the nuclei, synaptonemal complexes were observed, and consist of two lateral elements (36 nm) and a striated central element (22 nm) (Fig. 1A, C).

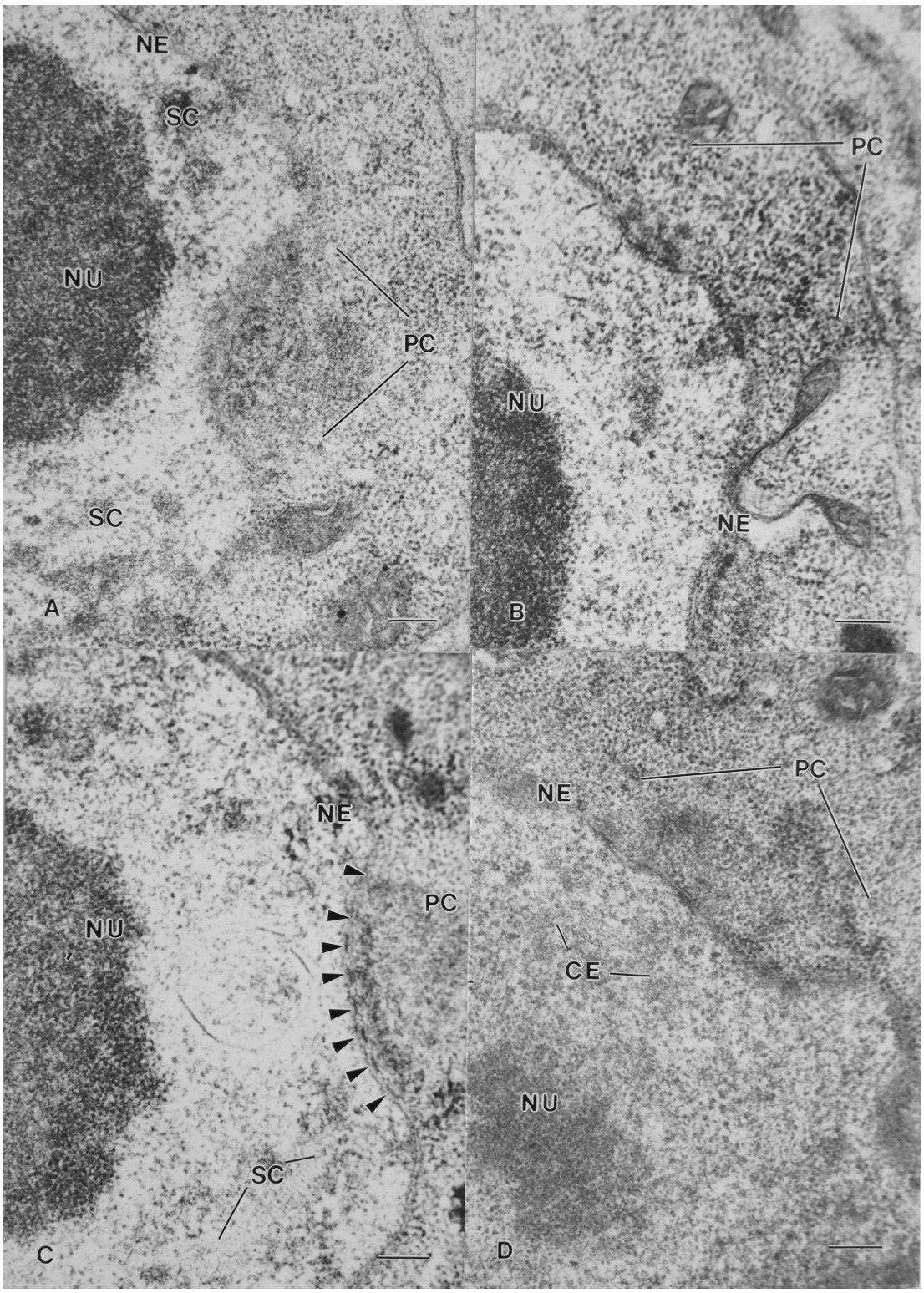

Fig. 1 A-D. Polycomplexes (PC) on the outside of the nucleus, consist of fibrillar material which will become organised in the lateral and central elements (CE) of the synaptonemal complex. They are attached to the nuclear pores of the nuclear envelope (NE) at leptotene and zygotene of meiosis prophase I in *C. elegans* hermaphrodites. The beginning formation of synaptonemal complexes (SC) can also be seen in the nucleoplasm. In (B), fibrillar material can be seen within the nucleus, across from the PCs (PC), and adjacent to the nuclear envelope. Nucleolus (NU). Scale bar = 0.1 μm.

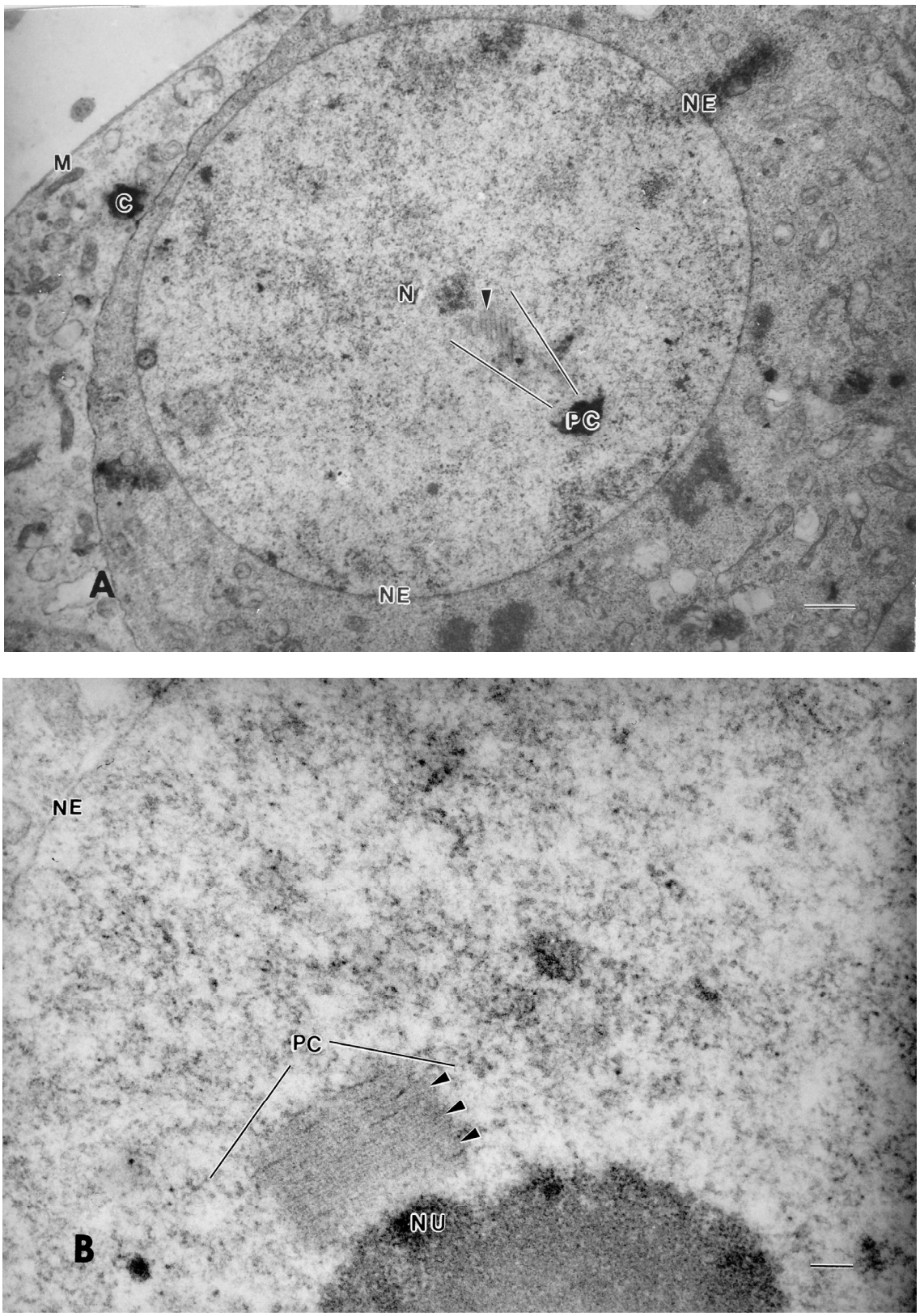

Fig. 2 A-B. Polycomplexes (PC), at the zygotene stage of meiosis prophase I in *C. elegans* hermaphrodites, are present within the nucleus. The PC consists of stacked arrays of lateral and central elements (arrowheads). Nucleolus (NU). Nuclear envelope (NE). Plasma membrane of the gonad (M). Cytoplasm of the gonad (C). Scale bar = 0.1 μm in Fig. 2A and 0.2 μm in Fig. 2B.

PCs (PC; Fig. 1) consisted of structured arrays of fibrillar material that has been demonstrated to become organised in the lateral and central elements (CE) of the synaptonemal complex (Fiil *et al.*, 1977; Ollinger *et al.*, 2005). Only a single PC was observed in any of the nuclei in the hermaphrodite. The PCs were attached to the nuclear pores of the nuclear envelope (NE) at leptotene and zygotene of meiosis prophase I in *C. elegans* hermaphrodites (Fig. 1C). This image is almost identical to Fig. 17 in Fiil *et al.* (1977) in *Ascaris*. The beginning formation of synaptonemal complexes (SC) can be seen in the nucleoplasm. In Fig. 1B, fibrillar material can be seen within the nucleus, across from the PCs (PC), and adjacent to the nuclear envelope. In some nuclei, the beginning of the formation of the SC occured simultaneously with the attachment of the fibrillar material and PC to the nuclear envelope (Fig. 1A, C, D). In addition, the FM was associated with the junction of the single telomeric end of the homologous chromosomes and SC that is capable of attaching to the nuclear envelope (Fig. 1C).

PCs, at the zygotene stage of meiosis prophase I in *C. elegans* hermaphrodites, are present within the nucleus (Fig. 2) and may be associated with the nucleolus and nuclear envelope. The PC consists of stacked arrays of lateral and central elements (arrowheads) whose dimensions are similar to that of the SC; *i.e.*, 100 nm in width. They are devoid of chromatin.

Fibrillar material was present in 40% of leptotene-zygotene nuclei, and 15% of zygotene-pachytene nuclei. PCs in the nucleoplasm were rare, occurring only in 10% of the nuclei examined. PCs and FM are not present after pachytene. They are also limited to the XX hermaphrodite and do not occur in any of the 100 nuclei examined in the XO males of *C. elegans*.

DISCUSSION

PCs have two distinct origins based on when they appear in the meiotic cell cycle. Premeiotic and early meiotic PCs originate as fibrillar material (FM) that is transported into the nucleus through the nuclear pores and organises into a recognisable PC (Fiil *et al.*, 1977). Post-pachytene PCs are the result of self-assembly of discarded SC fragments from the bivalents, or may be formed after aberrant *de novo* synthesis of SC proteins. PCs are associated with multiple nuclear and cytoplasmic structures and are randomly distributed in the cell.

FM, as seen in *Ascaris* (Fiil *et al.*, 1977; Merlin *et al.*, 2003), is also observed in *C. elegans* at the pre-pachytene stages of leptotene and zygotene. It is similar to FM observed in a number of other species and may represent unorganised, pre-synaptic precursors to the PCs. For example, in *Ascaris*, the earliest recognisable form of the PC is a filamentous bundle that may contain proteins of the central element of the SC (Fiil *et al.*, 1977). In addition, FM has been described in yeast as a PCs body and may be associated with the formation of PC (Moens *et al.*, 1981). In *Triticum*, the amount of fibrillar material present in the cell increased throughout premeiotic interphase and reached its highest level at leptotene. There was a gradual decrease as meiosis progressed through zygotene and FM was no longer present at pachytene (Bennett *et al.*, 1979). FM is also observed at the junction of the chromosome and inner nuclear envelope (NE) in *C. elegans* (Fig. 1A-D) and in wheat meiocytes (Bennett *et al.*, 1979), which may influence the attachment of the SC to the NE. Since the attachment of chromosome ends, observed as early as premeiotic interphase (Church, 1977), is considered a regular feature of meiotic prophase in the formation of a "bouquet" (where both ends of the chromosome are attached to the nuclear envelope) at pachytene (Moens, 1973), FM may influence the pairing of homologous chromosomes. This has particular significance in *C. elegans* since only one end of the chromosome can attach to the nuclear envelope and there is no bouquet (Goldstein, 1982). Fibrillar material may also play an important role in recognition of homologous chromosomes at greater distances (up to 3000 nm) than could be influenced by the SC (which is limited to 200 nm in distance). Such a mechanism must be considered in the three-dimensional architecture of the nucleus as well as segregation of the chromosomes and secondary movement of the telomeres.

PCs are limited in *C. elegans* to those cells in meiosis. They have not been observed in cells undergoing mitosis. This is similar to many other species in which PCs have been reported. Thus, commitment to meiosis may be essential prior to the production of those PCs observed prior to pachytene (Wettstein & Sotelo, 1971). In *C. elegans*, formation of the PCs occurs prior to pachytene and may occur when precursor subunits, such as SYP-1, reach critical concentrations. Control of formation of SCs from pools of proteins within the nucleus may reside in information coded in the DNA. In the absence of such a template, self-assembly of SC-like proteins prior to pachytene could account for formation of PCs. There are a number of nuclear proteins that have been identified that are related to chromosome structure and function, *e.g.*, Zip-1 and SYP-1

(Colaiacovo, 2006). In addition, topoisomerase II has been shown to be specific for the central axial region of the chromosome scaffold and LEs of the SC (Gasser *et al.*, 1986). These proteins may be part of the pool that would need to self-assemble to form the PC.

PC structure is conserved through evolution and consists of stacks of lateral elements (LE) that are 10 nm wide and are spaced approximately 100 nm apart, which are the same dimensions of the SC. The central region contains transverse filaments and a central element (30 nm), as first reported by Rasmussen (1975). The number of LEs can vary from 4-400 (as in *Acheta*; Jaworska & Lima-de-Faria, 1969). When two LEs are stacked (one from each PC subunit), the final dimensions are the same as one LE from the SC (Moses, 1968). This apparent paradox is resolved since the SC separates from the bivalent, and half of each LE remains attached to the chromosome, while the other half is incorporated into the PCs (Roth, 1966; del-Mazo & Gil-Aberdi, 1986).

PCs may form huge multiplex structures that require pairing of SC subunits to occur in tandem as well as side-by-side, as in *A. lumbricoides* (Fiil *et al.*, 1977). Regulation of SC substructure that normally exists when the SC is associated with chromatin, or when the central elements are being formed and inserted between the lateral elements, may be altered in the formation of the PC. Fusion of the LEs must occur even though these are structures that do not normally pair with each (Dudley, 1973). Such a binding of the LEs may occur if the molecular subunits of the LE undergo a conformational change that could alter their binding specificity (Fuge, 1979).

PCs are formed from the self-assembly of precursor subunits. Self-assembly does not require energy since associated subunits have a lower potential energy than free subunits. The formation of tobacco mosaic virus, for example, has been shown to occur *via* self-assembly when the levels of specific proteins are at a critical level (Zimmern & Butler, 1977). This association is analogous to the formation of PCs in *Ascaris* (Fiil *et al.*, 1977; Bogdanov, 1977, Merlin *et al*., 2003), whereby precocious, pre-pachytene synthesis of SC proteins that had built up to critical levels could precipitate in the form of PCs. The concept of out-of-phase synthesis was also proposed in *Drosophila* (Rasmussen, 1975) and yeast (Moens *et al*., 1981). The formation of excess protein pools prior to synapsis could be the result of errors in gene regulation, either by repression or activation (Stern & Hotta, 1983). Evidence of such pools was reported in *Aedes* where in vitro induction of PC formation was accomplished by changing the pH and/or osmolarity of the tissue culture medium (Wandall, 1980). In addition, ionizing radiation disturbed the enzymatic reaction in synapsis such that there was an increase in formation of variant forms of PCs (Sotelo & Wettstein, 1966).

Of note, is that PCs were not observed in this study to be present after pachytene, although they are prevalent in *A. lumbricoides* (Fiil *et al*., 1977) and *A. megalocephala* (Merlin *et al.,* 2003). Observations of post-pachytene PCs have been made in numerous organisms at the time of release of SC fragments from the bivalents and the association of these fragments into complex PCs (Dudley, 1973). An intact piece of SC could serve as a template (as in self-assembly) against which the stacking process could occur (Moses, 1969). The presence of PCs in meiotic mutants, aneuploids, or polyploids, could occur in the absence of a normal signal for transition from synapsis to diplotene or metaphase I or in the imbalance of genes. There may be an extended synthetic period in cells that have a disturbed pachytene.

There are biochemical similarities between the SC and PC: they both contain DNA (Moses, 1969), ribonucleoprotein (Esponda & Giminez-Martin, 1973) and specific histones that are rich in lysine and arginine (Wolstenholme & Meyer, 1966). In addition, lateral elements of the SC and PC have biochemical similarities to the nuclear half of the nuclear pore complex (Fiil & Moens, 1973). Amplification of DNA cistrons may result in the formation of PC in *Acheta* (Jaworska & Lima-de-Faria, 1969). Jaworska & Lima-de-Faria (1969) suggested that PCs were formed between extra gene copies of the homologous chromosome pair as a result of amplification of the rDNA cistrons in the DNA body. Amplification can also be defined as an increase in the number of available SC subunits and this can occur *via* a retardation in the degradation of released SC subunits after pachytene.

The random distribution of PCs within the cell results from their association with numerous nuclear and cytoplasmic structures, such as the nucleolus. There do not appear to be any specific active sites (or recognition sites) that are involved in this process. Rarely, non-membrane bound PCs have been observed in *A. suum,* but in those cases there was a strong affinity to form multiple PCs (Fiil *et al,* 1977). This excessive associative ability may reside in the altered nature of enzyme-regulating bonding or aberrant protein structure that results in the formation of multiple SCs (Fuge, 1979). It may also indicate that a template is required for initiation of

PC formation (Kelhoffner & Dietrich, 1983). The nature of this template is unknown, but may reside in recognition of membrane-bound proteins that are randomly distributed and common to diverse cell structures.

Numerous functions of the PC have been proposed. Since they are typically devoid of chromatin, they cannot function directly in the recombination process. However, synapsis and crossing over are two interrelated processes and PCs may play an important role in the recognition of homologues and the regulation of chromosomal segregation. Pairing of homologous chromosomes during meiosis is essential in the production of viable gametes. Long-range mechanisms of homologue recognition exist along with close-range (200 nm), site-by-site pairing during SC formation (Moens, 1968; Rasmussen, 1986). Chromosome pairing consists of at least four steps: *i*) recognition of homologous chromosomes; *ii*) prealignment or co-orientation of the homologues; *iii*) contact and initial pairing; and *iv*) complete synapsis along the bivalent (Rasmussen, 1986). The first two steps occur at greater distances than could be mediated by the SCs. Studies have revealed premeiotic associations of homologues that result in the alignment of the chromosomes prior to pachytene (Avivi & Feldman, 1973). These studies also reveal amorphous, fibrillar material, in both animals and plants that is associated with the telomeres of the chromosomes (Holm, 1977). Such chromosomal end attachment to the nuclear envelope is a regular feature of all cells and can begin as early as premeiotic interphase (Church, 1977). Thus, the first two steps of the mechanism of synapsis, in many organisms, include the association of chromosomes and fibrillar material.

In summary, this is the first study providing evidence of multiple synaptonemal complexes, or PCs, in N2 hermaphrodites of *C. elegans*. However, fibrillar material and PCs were not observed in the male, whereas the synaptonemal complexes from both forms were identical (Goldstein, 1982). This may be related to possible differences in control mechanisms of SC formation and homologous chromosome recognition between the two reproductive forms of *C. elegans*.

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REFERENCES

AVIVI, L. & FELDMAN, M. 1973. Mechanism of non-random chromosome placement in common wheat. *Proceedings of 4th International Wheat Genetics Symposium*, 627-633.

BENNETT, M., SMITH, J., SIMPSON, S. & WELLS, B. 1979. Intranuclear fibrillar material in cereal pollen mother cells. *Chromosoma* 71: 289-332.

BOGDANOV, Y. 1977. Formation of cytoplasmic synaptonemal complex like PCses at leptotene and normal synaptonemal complexes at zygotene in *Ascaris suum* male meiosis. *Chromosoma* 61: 1-21.

CHURCH, K. 1977. Chromosome ends and the nuclear envelope at premeiotic interphase in the male grasshopper *Brachystola magna* by 3-D, EM reconstruction. *Chromosoma* 64: 143-154.

COLAIACOVO, M. 2006. The many facets of SC function during *C. elegans* meiosis. *Chromosoma* 115: 195-211.

COUTEAU, F. & ZETKA, M. 2005 HTP-1 coordinates synaptonemal complex assembly with homolog alignment during meiosis in *C. elegans*. *Genes & Development* 19: 2744-2756.

DEL MAZO, J. & GILK-ALBERDI, L. 1986. Multistranded organization of the lateral elements of the synaptonemal complex in the rat and mouse. *Cytogenetics and Cell Genetics* 41: 219-224.

DUDLEY, P. 1973. Synaptonemal PCses in spermatocytes of the gooseneck barnacle, *Pollicipes polymerus* Sowerby. *Chromosoma* 40: 221-242.

ESPONDA, P. & GIMINEZ-MARTIN, G. 1973. Synaptonemal-like complexes in *Allium cepa* microspores. *Chromosoma* 42: 335-344.

FIIL, A. & MOENS, P. 1973. The development, structure and function of modified synaptonemal complexes in mosquito oocytes. *Chromosoma* 41: 37-62.

FIIL, A., GOLDSTEIN, P. & MOENS, P. 1977 Precocious formation of synaptonemal-like PCses and their subsequent fate in female *Ascaris suum*. *Chromosoma* 65: 21-35.

FUGE, H. 1979. A crystalloid component in the meiotic spindle. *Experimental Cell Research* 60: 309-313.

GASSNER, S., LAROCHE, T., FALQUET, J., BOY DE LA TOUR, E. & LAEMMLI, U. 1986. Metaphase

chromosome structure. Involvement of topoisomerase II. *Journal of Molecular Biology* 188: 613-629.

GILLIES, C. 1984. The synpatonemal complex in higher plants. *CRC Critical Reviews Plant Science* 2: 81-116.

GOLDSTEIN, P. 1978. Ultrastructural analysis of sex determination in *Ascaris lumbricoides* var. *suum*. *Chromosoma* 66: 59-69.

GOLDSTEIN, P. 1982. The synaptonemal complexes of *Caenorhabditis elegans*: Pachytene karyotype analysis of male and hermaphrodite Wild-type and *him* mutants. *Chromosoma* 86: 577-593.

GOLDSTEIN, P. 1985. The synaptonemal complexes of *C. elegans*: pachytene karyotype analysis of the Dp1 mutant and Disjunction Regulator Regions. *Chromosoma* 93: 177-182.

GOLDSTEIN, P. 1987. Aneuploidy in the normal life cycle of the nematode *Caenorhabditis elegans*. In: *Aneuploidy*, Part A: *Incidence and Etiology* (B. Vig & A. Sandberg. Eds.). pp. 189-204. NY, Alan R. Liss, Inc.

GOLDSTEIN, P. & SLATON, D. 1982. The synaptonemal complexes of *Caenorhabditis elegans*: Comparison of Wild-type and mutant strains and pachytene karyotype analysis of Wild-type. *Chromosoma* 84: 585-597.

GOLDSTEIN, P. & TRIANTAPHYYLOU, A. 1978. Occurrence of synaptonemal complexes and recombination nodules in a meiotic race of *Meloidogyne hapla* and their absence in a mitotic race. *Chromosoma* 68: 91-100.

HOLM, P. 1977. Three-dimensional reconstruction of chromosome pairing during the zygotene stage of meiosis in *Lilium longiflorum*. *Carlsberg Research Communication* 42: 103-151.

HOLM, P. & RASMUSSEN, S. 1983. Human meiosis IV. Chiasma formation in human spermatocytes. *Carlsberg Reseaarch Communication* 48: 415-456.

HORESH, O., SIMCHEN, G. & FRIEDMAN, A. 1979. Morphogenesis of the synapton during yeast meiosis. *Chromosoma* 75: 101-115.

JAWORSKA, H. & LIMA-DE-FARIA, A. 1969. Multiple synaptonemal complexes at the region of gene amplification in *Achaeta*. *Chromosoma* 28: 309-327.

KEHLHOFFNER, J. & DIETRICH, J. 1983. Synaptonemal complex and a new type of nuclear PCs in three higher plants: *Paeonia tennifolia*, *Paeonia delarayi* and *Tradescantia paludosa*. *Chromosoma* 88: 164-170.

LIU, J., YUAN, L., BRUNDELL, E., BJORKROTH, B. & DANEHOLT, B. 1996. Localization of the N-terminus of SCP1 to the central element of the synaptonemal complex and evidence for direct interactions between the N-terminal of SCP1 molecules organized head-to-head. *Experimental Cell Research* 226: 11-19.

MERLIN, J., GOLDSTEIN, A. & GOLDSTEIN, P. 2003. Meiotic structures in the animal-parasitic nematode *Ascaris megalocephala*: synaptonemal complexes, recombination nodules, and centrioles. *Journal of Nematology* 35: 223-227.

MOENS, P. 1968. The structure and function of the synaptonemal complex in *Lilium longiflorum* sporocytes. *Chromsoma* 23: 418-451.

MOENS, P. 1973. Quantitative electron microscopy of chromosome organization at meiotic prophase. *Cold Spring Harbor Symposium of Quantitative Biology* 38: 99-107.

MOENS, P., BARCLAY, B. & LITTLE, J. 1981. Nuclear morphology of yeast under thymidylate starvation. *Chromosoma* 82: 333-340.

MOSES, M. 1968. Synaptonemal complex. *Annual Review of Genetics* 2: 363-412.

MOSES, M. 1969. Structure and function of the synaptonemal complex. *Genetics* 61 (Suppl.): 41-52.

OLLINGER, R., ALSHEIMER, M. & BENAVENTE, R. 2005. Mammalian Protein SCP1 Forms Synaptonemal Complex-like Structures in the Absence of Meiotic Chromosomes. *Molecular Biology of the Cell* 16: 212-217.

RASMUSSEN, S. 1975. Synaptonemal PCs in *Drosophila melanogaster*. *Chromosoma* 54: 245-293.

RASMUSSEN, S. 1986. Initiation of synapsis and interlocking of chromosomes during zygotene in Bombyx spermatocytes. *Carlsberg Research Communication* 51: 401-432.

ROTH, T. 1966. Changes in the synaptonemal complex during meiotic prophase in mosquito oocytes. *Protoplasma* 61: 346-386.

SCHILD-PRUFERT, K., SAITO, T., SMOLIKOV, S., GU, Y., HINCAPIE, M., HILL, D., VIDAL, M., MCDONALD, K. & COLAIACOVO, M. 2011. Organization of the synaptonemal complex in *Caenorhabditis elegans*. *Genetics* 189: 411-421.

SOTELO, J. & TRUJILLO-CENOZ, O. 1960. Electron microscope study on spermatogenesis. Chromosome morphogenesis at the onset of meiosis and nuclear structure if early and late spermatids. *Zeitschrift für Zellforschung* 51: 243-277.

SOTELO, J. & WETTSTEIN, R. 1966. Fine structure of meiotic chromosomes. Comparative study on nine species of insects. *Chromosoma* 20: 234-250.

STERN, H. & HOTTA, Y. 1983. Meiotic aspects of chromosome organization. *Stadler Symposium* 15: 25-41.

SYM, M. & ROEDER, G.S. 1995. Zip1-induced changes in synaptonemal complex structure and PCs assembly. *Journal of Cell Biology* 128: 455-466.

VON WETTSTEIN, D., RASMUSSEN, S. & HOLM, P. 1984. The synaptonemal complex and genetic segregation. *Annual Review of Genetics* 18: 331-413.

WANDALL, A. 1980. In vitro induction of PCs formation. *European Journal of Cell Biology* 22: 26-35.

WESTERGAARD, M. & VON WETTSTEIN, D. 1972. The synaptonemal complex. *Annual Review of Genetics* 6: 71-110.

WETTSTEIN, R. & SOTELO, J. 1971. The molecular architecture of the synaptonemal complex. *Advances in Cell and Molecular Biology* 1: 109-152.

WOLSTENHOLME, R. & MEYER, G. 1966. Some facts concerning the nature and formation of axial core structures in spermatids of *Gryllus domesticus*. *Chromosoma* 18: 272-286.

ZHANG, W., MILEY, N., ZASTROW, M., MACQUEEN, A., SATO, A., NABESHIMA, K., MARTINEX-PEREZ, E. MLYNARCZYK-EVANS, S., CARLTON, P. & VILLENEUVE, A. 2012. HAL-2 promotes homologous pairing during *Caenorhabditis elegans* meiosis by antagonizing inhibitory effects of synaptonemal complex precursors. *PLOS Genetics* 8: 1-18.

ZIMMERN, D. & BUTLER, P. 1977. The isolation of tobacco mosaic virus RNA fragments containing the origin for viral assembly. *Cell* 11: 455-462.

Goldstein, P. Множественные синаптонемные комплексы (поликомплексы) в гермафродитах дикой линии *Caenorhabditis elegans* и их отсутствие у самцов.

Резюме. Синаптонемные комплексы представляют собой весьма эволюционно-консервативные и стабильные в своем строении и функциях структуры. Объединенные вместе, эти структуры формируют суперструктуры, известные под названием «множественные синаптонемные комплексы» или «поликомплексы» (ПК). К настоящему времени эти поликомплексы описаны у более чем семидесяти самых разнообразных организмов, в том числе, и у нематод. Во время стадий лептотены и зиготены хроматино-подобный материал, известный как «внеклеточный фибриллярный материал» (ФМ), обнаруживается вблизи ядерной оболочки (ЯО). На стадии пахитены ФМ виден уже внутри ЯО, где он тесно ассоциирован с теломерами и осевой частью синаптонемных комплексов. Присутствие поликомплексов у гермафродитов (генотип XX) дикой линии *Caenorhabditis elegans*, как и у других организмов, приурочено исключительно к фазам мейоза и тканям нематоды, происходящим из зародышевого пути. Хотя поликомплексы могут присутствовать до или после формирования синаптонемных комплексов у других нематод (например, у *Ascaris*), их облик и функции различны на этих разных стадиях. У *C. elegans* поликомплексы наблюдаются только до стадии пахитены – в момент смены лептотены на зиготену, а затем полностью исчезают. Структуры и биохимический состав поликомплексов сходны с таковыми у синаптонемных комплексов. Их основной элемент состоит из трех частей, с двумя боковыми и одним центральным участками. Внутри последнего различимы поперечные структуры. Белок SYP-1 выявляется в центральной части синаптонемного комплекса у *C. elegans*, наряду с белками HTP-1 и HAL-2. Все эти белки являются неотъемлемой частью в организации поликомплексов. Поликомплексы никогда не были выявлены у самцов *C. elegans* (генотип XO), что указывает на различные уровни в степени контроля спаривания гомологичных хромосом и их прикрепления к оболочке ядра на протяжении профазы мейоза.