



Chromosome organization: curiosity in diversity

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Abstract

This article attempts to apprise curiosities attendant in organizational diversity and behaviour of chromosomes from academic and utilitarian prospective, pinpointing certain uncommon but unique features. The chromosomes, comprised of DNA and proteins are the major component of the nucleus in Eukaryotes, wherein about 4 cm long DNA fiber is compacted to form a chromosome of 1 μm in diameter and 10 μm in length. Chromosomes have defined territories in the nucleus and serve as the continuum for sustenance of heredity and variation both at asexual and sexual level realised through mitotic and meiotic division, respectively. Notwithstanding the above commonalities, the plants and animals significantly differ for their chromosome and cellular organization. The animal cell lacks cell-wall but owe dynamically organized well differentiated linkage groups with specific location of repeat families, in clear contrast to plants where cell has a well-defined cell-wall but lacks repeat family-based precise differentiation between the linkage groups. Curiously, the plant systems offer unique *in planta* opportunities to realize variation through the incidence of polyploidy, intergenomic hybridity and genomic orientation, kinetochore function, de novo somatic diversity, polysomaty, endopolyploidy and polyteny in differentiating tissues, B chromosomes that at times become a source of variation, adaptation and speciation. Drastic variations are encountered in form, function, and number of chromosomes in plants, ranging from $n=2$ in *Brachyscome dichromosomatica* to $n=320$ in *Sedum suaveolens* (Crassulaceae), at family level from $n=4$ to 120 in the Brassicaceae, and at genus level from $n=2$ –45 in *Brachyscome* (Asteraceae)—in angiosperms; to $n=720$ in ferns. However, the cell size does matter to decide the size of chromosomes a cell can accommodate. One of the key realizations in the “genomics era” is that polyploidy is ubiquitous in plants, and that all modern flowering plant genomes are derived from processes set in motion by a history of repeated, episodic whole-genome doubling, or polyploidy. Viewpoints are underway that foresee the dominance of perennial herbs and prominence of auto-polyploids in the coming centuries if the present global trend of climate change continues at the given fast pace in Anthropocene. However, when divergent diploid genomes are combined to form an allopolyploid genome, there are instances of genomic/genetic changes to realize genome/chromosome elimination and/or gene silencing to assuage hybrid stabilization. Whereas inactivation/elimination of centromeric histones lead to chromosome/genome elimination, but spatial position of the partner genomes is largely relative to the size of their chromosomes and centromeres that facilitate intergenomic fixation.

Keywords Chromosome diversity · Chromosomal curiosities · Chromosomes in differentiation · Polyteny and endopolyploidy · Chromosomes in speciation and adaptation · Polyploidy and Climate Change · Genomic Territories · Interspecific hybridization

This article is dedicated to my revered mentor Prof. AK Sharma who propounded the ‘Concept of Chromosome Dynamism’—a theme around which this article is structured, as a tribute to commemorate his Birth Centenary. It is based on the Presidential address delivered on 16 October 2024 during 47th All India Botanical Conference held at CCSU, Meerut.

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Introduction

With the introduction of the word ‘Chromosome’ in 1888 [74], Polyploidy in 1916 [78]), role of polyploidy in evolution [77] and recognition of DNA Double helix in 1953 [75] as the basic functional and structural component of chromosome, and establishment of its semiconservative replication in 1957 [68], the basic principles of Cytogenetics are said to have been established by 1958 [56]. Notwithstanding progressive fast developments in cytogenetics, it may sound quite curious that for man, even the correct chromosome counts could be established as late as 1956 [69], although significant progress in the field was in place for plants and insects much earlier. We now know that the chromosomes, comprised of DNA and proteins are the major component of the nucleus in Eukaryotes, wherein about 4 cm long DNA fiber is compacted to form a chromosome of 1 μm in diameter and 10 μm in length [47]. Several breakthroughs in chromosome technologies have since taken place, that have enabled precise identification of chromosomes and chromosome segments, including telomere and centromere, under in situ and isolated conditions, and behaviour of chromosomes at the organism and population level. All plants and animals follow the standard principles of $2n$ number in somatic cells and $1n$ in gametes.

Further, certain unique developmental and structural variations, e.g. formation of polytene chromosomes in the salivary glands of insects, such as in *Drosophila*, and the path-breaking discovery of bridge-breakage-fusion cycle and *Ac/Ds* controlling elements in maize by McClintock, multiple translocations (Renner’s complex) in *Oenothera/Tradescantia* etc. maintained through balanced lethal system, well defined sex chromosomes in animals and lack of recombination in male sex determination chromosomes, *Ph* gene for regulation of pairing in wheat, are some of the unique feature that are common knowledge described in text books on cytogenetics/genetics. Therefore, these unique but well-known features are kept outside the scope of this article.

Schubert [56] while discussing the past developments has raised several open questions touching the field of cytology and cytogenetics that need to be answered in coming years. Way back in 1978, Sharma [60] while discussing the ‘Chage in Chromosome Concept’ pinpointed that during organogenesis, the chromosomes while maintaining the basic genetic skeleton, may undergo variation in structure and chemical components, thus exhibiting dynamism. Endomitotic replication, de novo somatic diversity, polysomaty, and polyteny in differentiating tissues, addition, loss and inactivation of heterochromatic segments have been correlated with adaptation and alteration in chromosome size. As such there are several apparent unique and deviant features encountered in chromosome behaviour

that invoke chromosome diversity in curious manner. This article is focused on a few such curious features that are uncommon but have far reaching implications facilitating unique genomic and genetic change. The same are briefly presented here:

Chromosome analysis in animals versus plants—some core differences

Whereas, tremendous progress was achieved in the study and analysis of plant chromosome in the initial stages of investigation with an early advent of staining techniques, but progress in animal chromosome analysis has far advanced owing to technical ease, on account of organizational differences listed below. Curiously, the correct chromosome number in man was established as late as in 1956 [69], that too with the technical support of a plant scientist. However, plant chromosome analyses have significantly contributed in understanding the role of chromosomes in evolution, since the incidence of polyploidy is ubiquitous in plants and easy to manipulate but less common in animals.

Animal chromosomes Developmental fate of cell is determined right at the initiation of zygotic differentiation into germ lines. Chromosome study is much simpler because there is no cell wall and dividing cells are easily achieved as cell suspension to prepare cell smears. DNA repeats are clustered into discrete linkage groups; hence every linkage group is unique for its repeat families that can facilitate discrete chromosome painting. There is well defined chromosome-based sex determination.

Plant chromosomes Cell differentiation and organogenesis is a temporal process. Chromosome study is much more difficult on account of technical difficulty posed by the presence of cell wall as well as on account of dividing cells embedded in well bound tissue that hinders easy release of free cells. DNA repeats are dispersed all across the genome, hence differentiation of linkage groups is quite difficult using DNA probes. There is poorly defined chromosome-based sex determination.

Chromosome territories

Way back, I came across a paper published in *Chromosoma* by Wagenaar [73] that the chromosomes at somatic prophase exhibit end-to-end connectivity, and the same was substantiated by Fussell [21]. Through a follow-up

study it was revealed that chromosomes maintain proximity with their homologous partner, sporting spatial association between the chromosomes and exhibit Rabl orientation throughout division cycle [36]. Subsequently, precise details about the chromosome territories in the Nucleus have been advanced, but all along a central theme of Rabl orientation or Rosette, contributing to the establishment of different configurations and 3D folding [66]. This has repercussions in cross talk and epigenetic control between homologous partners and their closely associated sister chromosomes in an overall chromosome organization in the nuclear territory, and large transcriptional reprogramming.

Tolerance limit for chromosome arm length for normal development of an organism—there is an upper and lower limit.

Using a series of field bean lines with karyotypes of considerable variation in length of individual chromosomes, Schubert and Oud [57] proposed that as a rule there is a clearly definable limit for chromosome arm length, suggesting that for normal development of an organism, the longest chromosome arm must not exceed half of the average length of the spindle axis at telophase, otherwise the termini of sister chromatids shall not separate during mitotic metaphase and cause micronuclei and apoptosis. Similarly, a reverse question is asked—are there lower limits of chromosome size for stable mitotic and meiotic segregation. It is suggested that to accommodate a functional centromere and telomere, the chromosome size between 120 to 500 kb may be desirable as demonstrated using artificial yeast chromosomes by Niwa et al. [51].

Diversity and variation in chromosome number in plants

Drastic variations are encountered in form, function, and number of chromosomes in plants, ranging from $n=2$ in *Brachyscome dichromosomatica* to $n=320$ in *Sedum suaveolens* (Crassulaceae), at family level from $n=4$ to 120 in the Brassicaceae, and at genus level from $n=2$ to 45 in *Brachyscome* (Asteraceae)—in angiosperms; to $n=720$ in ferns. For further details—see Vimala et al. [70]. Wide occurrence of B chromosomes is another feature encountered in plants [31]. Initially thought to have no regulatory or evolutionary significance, the importance of Bs is emerging as a new entity for its significance in adaption and epigenetics.

Sister chromatid exchange—a valuable resource for study of mutagenesis.

Whereas, physical exchange of chromatids between homologous chromosomes during meiotic cross over is an established biological feature to facilitate genetic recombination and variation, but sister chromatid exchanges do not happen during meiotic recombination. Nevertheless, the incidences of double sized di-centric ring chromosomes in somatic cells of maize clearly point out that such ring chromosome may have arisen from sister chromatid exchanges [45]. Feeding Tritium labelled DNA to the dividing cells Taylor [67] demonstrated that replicating sister chromatid could be differentiated in the autoradiograms, and that there were incidences of sister chromatid exchanges in the mitotic chromosomes. The technique has since been perfected for animal and plant systems, replacing radioactive DNA labels to Fluorochrome DNA labels, differentially detected by Geimsa staining, what is commonly known as FPG technique i.e. Fluorescence plus Geimsa [52, 58].

Study of such reciprocal interchange between chromatids (Sister Chromatid Exchange—SCE) is being extensively applied as a rapid and sensitive and quantitative assay for genetic damage, and mutational analysis [14]. Only an introductory information is provided here to pinpoint the curious feature of sister chromatid exchange, but more information is available in literature.

Recognition of chromosomes from fossilized organs:

Fossilization processes tend to destroy fine-cell structure, but examples of exceptionally well-preserved subcellular structures, including nuclei and even chromosomes in various stages of cell division that have remained unchanged for 115–180 million years are reported from Jurassic deposits. Notable examples are from Rajmahal hills, India for the sporangium of Pteridophyte [72], and even in a seed plant e.g. *Pentoxylon*—a unique Gymnosperm [12], and in ferns from Sweden [11]. The nuclei of the chromosomes show a brownish-yellow color imparted as a result of the ferrous oxide present in the chert matrix itself with a high-resolution contrast without staining. The latter closely resemble the fossil nuclei of extant cinnamon ferns, *Osmundastrum cinnamomea*, which indicates that this group of ferns has remained virtually unchanged for 180 million years.

Chromosome structure, cell division and organogenesis

Whereas basic genetic make-up is necessary for hereditary stability, but it remains a curiosity that the chromosome constituents change their pattern during different phases of development, invoking variation in DNA and proteins in the metabolically active cells from organ to organ.

(a) Variation in DNA and chromosome size during organogenesis

Way back in 1955 Holmes et al. [26] reported steady increase in the mean DNA content per cell with distance from root apex, being 30 per cent greater in the proximal segment mainly composed of fully differentiated cells, than the terminal meristematic segment.

Lyndon [44] has shown that large differences in size and mass between prophase nuclei of root and shoot in *Pisum sativum* are accompanied by changes in cell cycle time. The smaller nuclei with less mass divide more slowly. On the other side an increase in chromosome size/volume/dry mass to the tune of over 50% in root tips meristem of rye and *Allium cepa* was found to be induced by growing the plants in phosphorous containing solutions, of course the DNA amount remained constant [9]. A curious instance of large natural variation in chromosome size to the order of three-fold between the cells in plant meristems of different

ages has been reported in a male sterile plant of *Vicia faba* (Fig. 1). But, this enhanced variation in chromosome volume was attributed to increased nuclear protein content [8]. Nevertheless, variation in chromosome size did impact the mitotic cell cycle. The meristematic cells in the main root with larger chromosome volume attributed to higher protein content have shorter mitotic cycle, meaning thereby higher metabolic activity, and the cells in lateral roots with lower chromosome volume and lower protein content evince longer mitotic cycle and lower metabolic activity [10].

However, a clearcut evidence about variation in DNA content in the active nuclei of various plant organs has been provided by Banerjee and Sharma [4]. Experimental data presented by them on estimation of DNA through cytophotometry at in situ level from cytological smears, as well as from nuclei after extraction from tissues, representing three distinct developmental zones—root meristem, differentiated zone and shoot meristem, on a range of plant species, namely: *Pisum sativum*, *Lens esculenta*, *Trigonella foenum-graecum*, *Nigella sativa*, *Hordeum vulgare* and *Aloe vera*, demonstrated noticeable variation in DNA amounts to the order of ~1.00: 1.49: 0.81, in the root meristem, differentiating zone and shoot meristem, respectively i.e., least in the shoot tip. Such observations apparently suggest that the basic amount of DNA necessary for genetic stability is present in the shoot-tip region, wherefrom differential DNA amplification may play a role in initiation of organ differentiation [4]. Bassi [6] based on critical analysis of existing literature underscoring the occurrence of quantitative DNA variations during plant development stated that the plant genome is not so ‘quantitatively static’, instead characterized by a dynamic plasticity, and the role of repeated DNA sequences in the plant development seem to be much more active, inferring dynamic chemical makeup [60].

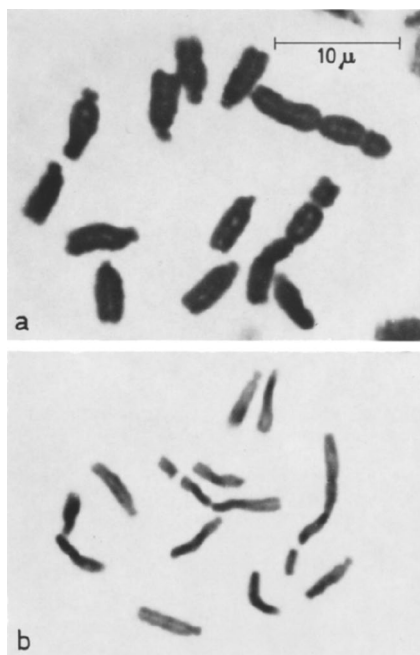


Fig. 1 Root tip metaphase chromosomes of *Vicia faba* from a main root at: **a** 7 days and **b** a lateral rootlet at 38 days from the same seedlings. The difference in volume is of the order $\times 3$. Reproduced with permission from [8]

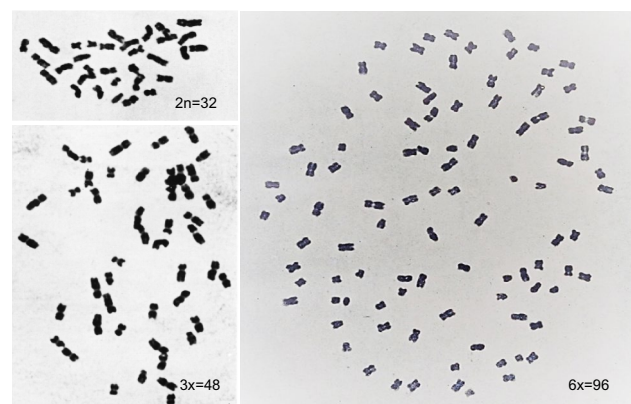


Fig. 2 Ontogenic endopolyploidy in endosperm of coconut, *Cocos nucifera* exhibits ploidy layers of 3 $\times$, 6 $\times$, 12 $\times$ and so on; reproduced from [1] and group. The somatic number in this species 2=32

(b) Differentiation, Ontogeny and cell division

There are well defined standard cell division phases commensurate with the progression of cell cycle. However as pointed above, the cyclic changes in Histone/DNA ratio during development greatly impact differentiation. Both progressive duplication and regressive reduction have been encountered under specific conditions. The following two unique examples may be worth discussion here:

(i) Progressive somatic chromosome duplication in Coconut endosperm

From the series of publications Abraham's group [1–3] has reported progressive euploid somatic duplication cycles in the endosperm of Coconut, progressing from periphery to centre representing 3 $\times$, 6 $\times$ and 12 $\times$ and so on (Fig. 2). Such phenomenon is also known to be occurring during endosperm development in the other related taxa.

(ii) Retrogressive somatic reduction in apogeotropic roots of Cycas

Recurrent somatic reduction is a normal ontogenetic process in apogeotropic roots of cycads, which develop into dichotomously branching coralloid masses. First observed in *Cycas revoluta*, Storey [65] has reported such somatic reduction in several taxa of Cycads, where cells with reduced somatic chromosome number were seen making consecutive rings serially progressing towards periphery in the differentiated cortical tissue lying midway between the pericycle and the epidermis. Such reduced cells are said to be serving as filters among the large cells that are charged with slime during maturation.

Whereas, no specific description has been provided to explain the curious observation reported in (i) and (ii) above, but the following observations made on the histone/DNA ratio during development and maturation may be worth considering for further exploration in the above context.

Innocenti and Avanzi [28] reported four morphologically distinguishable cell division patterns in *Allium cepa* roots in the immature metaxylem. It is observed that during metaxylem maturation, cells close to the region of the apical initials undergo a process of chromosome endoreduplication, and in the histological region between 800 and 1200 μ from the root tip show gene amplification of the nucleolar organizing region, and in the region 1200 and 2000 μ from the root tip show extrusion of the nucleolus from the nucleus (about 30% of cells show such phenomenon), followed by de-spiralized chromatin appearance. Further analysis of nuclear DNA and histone content in procambial cells with developing metaxylem in *Allium cepa* root tip, showed that histones/DNA ratio is not constant in all the stages, instead highest during endoreduplication process [27].

(c) Dynamism as expressed by accessory chromosomes

Generally considered non-essential and having no obvious effect on the phenotype and no relationship with environmental factors, the significance of B chromosomes

increased after their discovery in maize, and an exhaustive account on their occurrence is provided in various reviews—see Jones [31].

A classic example of adaptive and buffering action of B chromosomes is provided by Sharma and Aiyangar [61] from a systematic study conducted on B+ and non-B genotypes occurring in natural habitats. In *Allium stracheyii* found in Darjeeling (located in the east Himalayas), they [61] recorded the occurrence of up to 8B chromosomes in diploids and their complete absence in polyploid individuals of the same species. These diploid individuals, when grown under tropical conditions, were gradually converted into polyploids with the complete elimination of B chromosomes. Induction of polyploidy and subsequent elimination of Bs could be avoided by growing plants in artificial environment with lower temperature, representing the Himalayan conditions [61]. This behaviour is taken as an index that B chromosomes confer certain adaptive advantage at the diploid level. It is surmised that with the onset of polyploidy, which increases tolerance of the species through increased gene dosage, the B chromosome become redundant and are eliminated [60]. Another example of B chromosome dynamism worth citing is that B chromosomes from *Aegilops* species can compensate for the absence of chromosome 5B, known to suppress homoeologous pairing—Riley and Chapman [55], by preventing or reducing homoeologous pairing [54].

Lately, the so called non-essential B chromosomes have found a novel application in plant breeding. The reconstructed miniB chromosome loaded with expressed reporter gene has been found to be an effective system to sexually transmit the reporter genes across generation, and thus emerging as an effective recombinase tool kit, mitigating the drawbacks associated with conventional transgenic approach [43].

Polyteny, endopolyploidy and differentiation

Whereas mitotic and meiotic cell division are the essential elements of reproduction cycle, but certain curious events deviating from the standard are encountered during development and differentiation under special conditions.

- (i) *Definition and occurrence* Modification in mitotic cell cycle during interphase is known to cause formation of giant chromosomes/nuclei during growth and development in certain tissues and organs [50]. These cells execute normal S phases, using a G1-S regulatory apparatus similar to the one used by mitotic cells, but their capability to segregate chromosomes has been suppressed, and the nucleus initiates a new G1 phase starting a new cycle, successively replicating

their genomes without segregating chromosomes during mitosis what is termed as ‘endocycle’ [18, 50] or ‘endoreduplication’ [16], giving rise to endopolyploidy with multistranded/ polytenic chromosomes. Such giant/polytenic chromosomes are said to have been formed in specialized tissues demanding enhanced transcription to realize high metabolic efficiency. Such polytechnic giant chromosomes were initially reported in salivary glands of dipteran larva, e.g. *Drosophila* and are quite common in other insects and birds, but not so common in plants. An account of the occurrence of polytechnic chromosomes in specialized cells of certain plants, e.g. suspensor cells, tapetal cells, and others [15, 17, 49, 50]. Another means of in situ chromosome duplication is ‘endomitotic cycle (endomitosis)’ where chromatids replicate followed by sister chromatic separation and condensation (endometaphase) and decondense to assume interphase nuclear structure thus forming endopolyploid cell [16, 50]. Such cycles are quite common during the tapetal differentiation constituting either multinucleate cells with more than one diploid nucleus, and/or mononucleate cells with a single polyploid nuclei and mono- or binucleate cells with one or two polytene nuclei [15, 35].

- (ii) *Necessity and strategy* Nagl [48] has listed a large number of species, both plants and animals, which undergo such endomitotic replication. In plants, such a behaviour is quite common in embryonic suspensor and endosperm while they are at the threshold of high metabolic activity. This is in conformity that formation of polytenic or endopolyploid nuclei/endomitotic replication is often accompanied by increase in DNA content, suggesting that such endowed tissue needs several copies of most genes required for enhanced transcription activity to supply specific substances with progressive development and differentiation [15, 48], and others cited therein.
- (iii) *Experimental demonstration of polyteny and chromatid endoreduplication during differentiation* The differentiation of organs is initiated after cessation of active cell division. In the adult or mature tissue, the gene action necessary for enzyme protein synthesis is at the optimum level but the nuclei in differentiated tissue do not show active mitosis [60]. As pointed out above under the section ‘[Chromosome structure, cell division and organogenesis](#)’ there are experimental evidence underpinning the increase in DNA amount and histone: DNA balance in the differentiated mature tissues, and organ to organ. Further validation of such inferences has been physically demonstrated by inducing cell divi-

sion in mature tissues. While increase in nuclear size could be taken as a gross estimate of endopolyploidy, but direct categorical evidences have been provided—see Sharma [60]. Presence of metaphase chromosomes with four strands or even multi-strands against the standard two, has been clearly demonstrated in mature somatic tissues after induction of cell division [5, 60]—Fig. 3. Evans and Van't Hof [19] have, on the basis of measurements of relative DNA values of different species, suggested that cell differentiation can occur without polyploidy. They recorded polyploidy in sepals, pods, pistils and stamens but not in petals of *Pisum*; in leaves but not in roots of *Triticum* and no polyploid in *Helianthus*. Nagl [48] based on such observations and other similar records has suggested that increase or differential amplification of basic nuclear DNA achieved through repetitive DNA, generative polyploidy, etc. is often needed for differentiation and specialized function of certain cells in Eukaryotes.

Somatic mosaics and fixity in chromosome number—a novel means of speciation for vegetatively reproducing species

In a range of plant taxa, where vegetative propagation is obligatory, no constancy in the chromosome number in the somatic cells, even in the same root-tip is found. As such the somatic tissue represents a mosaic of chromosome complements in which the normal complement occurs in the maximum frequency [62, 63]. Such observations have been made in hundreds of taxa across genera and family that are deficient for sexual reproduction, thereby limiting the chances of creation of new combinations and variability so necessary for diversification. Nevertheless, such species continue to produce new genotypes and cultivars, indicating that they have developed alternative methods of generating variability [60].

Experimental evidence obtained on a large number of taxa suggest that such a regular occurrence of inconstancy in the chromosome complement plays a significant role in the origin of new genotypes through their participation in the formation of new daughter shoots. Whereas, cells with abnormal chromosome number may not pass through meiotic sieve to enter into germline for sexual reproduction, but where mode of propagation is vegetative such chromosomally variant somatic cells may enter into the development of new shoots. This could lead to variation and speciation, as conceived in the ‘new concept of speciation’ propounded by Sharma [59, 62].

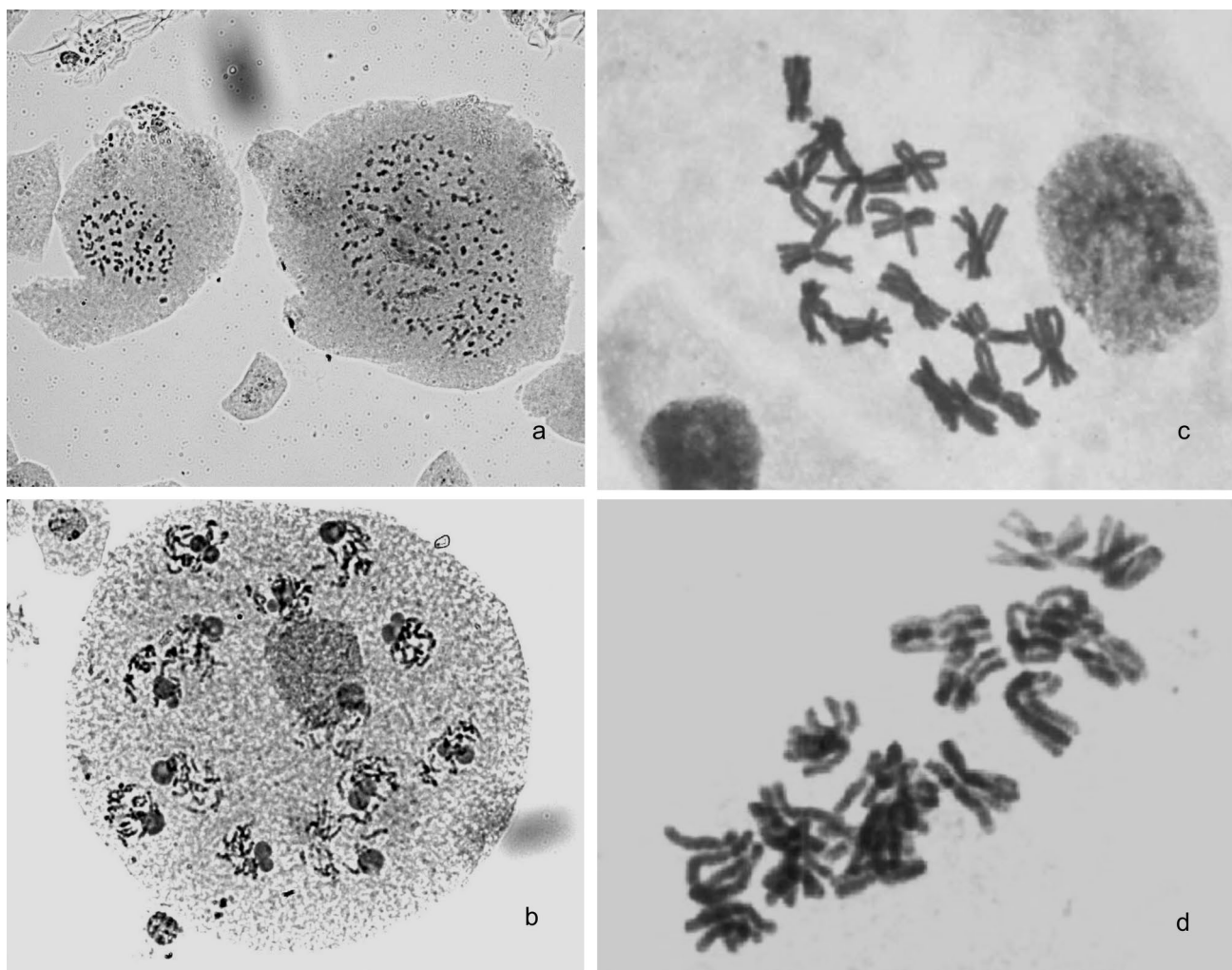


Fig. 3 Illustration of endopolyploidy and polyteny in plants. **a** Restitution endopolyploid, **b** acytokinetic multinucleate endopolyploid—observed in Tapetal cells; **c** *Allium cepa* somatic metaphase—control, showing diplo-chromosomes i.e. two chromatids, and **d** somatic

metaphase from differentiated mature tissue—showing four stranded chromosome i.e. one round of polytechnic replication. *Source:* **b** from Lavania et al. [35], and **d**—courtesy YK Bansal

Incidences of Mega Chromosomes, and evolutionary cyclic chromosome changes during callus culture

It is a well recorded fact that the stressed environment caused under in vitro culture conditions brings about genetic and cytological abnormalities—see review by Bayliss [7]. Lavania and Srivastava [38, 39] provided categorical instance of numerical and structural changes encountered during callus subcultures suggesting that only balanced euploid variation could pass through morphogenetic sieve during organogenesis, including cycles of polyploidization. Such changes could be considered parallel to evolutionary changes encountered in ‘Nature’ over geological time scale. Another systematic cytological study conducted on subcultures raised from root-tip

meristem of *Allium porum* exhibited all sorts of structural chromosomal variations including dicentric and polycentric chromosomes, and typical instances of incidences of occurrence of Mega-chromosomes where one of the arms was found to be excessively long to the tune of approximately ten times of a normal chromosome [30]. Formation of megachromosomes had earlier been reported in series of interspecific hybrids of *Nicotiana* spp. [23, 24] and others cited therein, suggesting that chromosome arms having the inserted heterochromatic blocks can occasionally undergo great enlargement to form chromosomes of astonishing length. It is suggested that such megachromosomes arise de novo in interphase preceding mitosis in which they are subsequently observed [24]. However, in all the reported instances of megachromosome occurrence, none of them could be transmitted to the next cellular progeny, perhaps

the reason lies in the limit of chromosome arm size as inferred by Schubert and Oud [57].

However, de novo formation of megachromosome in mouse consequent to large scale amplification of pericentric region of mouse chromosome in cell cultures in the cell lines obtained from the fusion of mouse and Chinese hamster is quite common [32]. Only a passing reference is provided here for the sake of recording curiosity and further details are available in the related literature.

Premature chromosome condensation

The mitotic cell division in any organism follows a standard route of condensation and de-condensation cycle, where individual chromosomes at interphase are not so well differentiated, unlike in meiotic pachytene where chromosomes are reasonably differentiated to enable physical study of chromosome analysis and behaviour. However, premature chromosome condensation of interphase chromosomes could allow an improved means of chromosome analysis at cell level. Curious enough it is observed that when a cell at interphase is fused with a mitotic cell, the fusion product results into “premature chromosome condensation” (PCC) of interphase chromosomes exhibiting their pulverised appearance in the somatic cell [64]. In the initial stages of discovery, such PPC was realized as Sendai virus induced PCC (virus-mediated PCC), but techniques for drug induced PCC by protein phosphatase inhibitors have now been developed, opening new means of detection of chromosome associated changes and detailed analysis of interphase chromosomes that have diagnostic applications from basic cell biology to practical applications in radiation biology [25]. A new area of experimental analysis is advancing. A detailed account is avoided here considering that further discussion may be outside the scope of this article on curiosities.

Interspecific hybrids, genomic territories and chromosome elimination

Interspecific hybridization has been a major evolutionary force in realizing new genomic combinations, as a natural force, as well as, by means of experimental manipulation facilitating genetic enhancement. Obvious questions that dominate the mind of geneticists’ dwell around the prospective success of interspecific hybrids, their genetic and breeding implications and the factors affecting their success. With the technical advances made in the genomic

technologies, it has been amply demonstrated that in any interspecific hybrid combination, the partner genomes occupy definite spatial position in the combined nucleus forming sort of concentric rings maintaining their territorial identity. The spatial position of the partner genomes and their stability in hybrid genome is largely dependent on the relative size of their chromosomes and centromeres that are linked to cell cycle progression. The genome occupying peripheral position is most likely to exert sub-genome dominance over the central partner. On the application side the wide hybridization has been found useful in haploid formation through chromosome elimination system, where the genomic partner with weaker centromere is destined to be eliminated. Further advances have been made whereby manipulation of Centromeric histones to realize null centromere is being used towards the directed development of haploids. A more specific account on these aspects has been discussed by Vimala and Lavania [71], hence a detailed description is avoided here, but an overview is given here to underpin the curiosity associated with genomic territories and genome elimination in the interspecific hybrids.

Polyploidy and body size and fixation of heterozygosity

It is generally believed that polyploidy brings about increase in cell size by a factor of about 1.5 times, bringing enlargement of vegetative organs. However, it is observed that enlargement of organs is somewhat offset by reduction in cell number, thus adjusting the expected increase in body size. We attempted to address this curiosity using clonal polyploids of diverse species of aromatic grass, *Cymbopogon* that are linked via a common secondary metabolite pathway but envisage limitation in pathway progress. The findings demonstrated that there is increase in cell size and the essential oil concentration in the polyploids in all the species, but their vegetative growth exhibits different and clearly diverse patterns, i.e. the species invoking longer metabolic route instead showed reduced vegetative growth—say reduced body size, and the one that stopped at the initial steps of the pathway expressed vigorous vegetative growth, suggesting that there is differential effect of polyploidy on body size; longer the metabolic route more stress on growth and vice versa. A detailed account to this inference is given in Lavania et al. [41].

Another area of curious interest is whether polyploidy can facilitate fixation of heterozygosity. Based on exhaustive meiotic analysis on diploid/tetraploid correlation conducted over a range of species, it was inferred that the progenitor diploid species harbouring distal chiasma

formation and small sized chromosomes when converted to tetraploid, behave like diploid with regular meiotic segregation. Such a situation is likely to maintain the heterozygous character of the progenitor diploid in the tetraploid owing to tetrasomy mode of inheritance—thus facilitating realization of fixation of heterozygosity [33, 40].

Wonderous cycles of Genomic Duplication and polyploidy in climate change regime—we may see more short-statured herbaceous plants in future

Notwithstanding the recognition of polyploidy since 1916 [78], the existence of ancient gene duplication was established from the comprehensive phylogenomic analyses of sequenced plant genomes and more than 12.6 million new expressed-sequence-tag sequences implicating two WGDs (Whole Genome Duplication) in ancestral lineages shortly before the diversification of extant seed plants and extant angiosperms, respectively [29]. Identification of large syntenic blocks of genes within genomes provided strong evidence that angiosperm genome has experienced multiple episodes of polyploidy events, what is now termed as ‘Wonderous cycles of Genomic Duplication’ [76].

Polyploid speciation that generate genetic variation and facilitate adaptation to new environments is considered a long-term evolutionary survival strategy [13], exemplified by the fact that during the fifth mass extinction at the end of the Cretaceous, many flowering plants escaped extinction by duplicating their genomes [20] and then evolved into dominant terrestrial plant lineages [29]. Levin [42] opines that new polyploids enabling novel plant traits and enhanced physiological functions and environmental tolerance may competitively replace their ancestors, or they may invade new territories.

Analysis of empirical data recorded on the incidence of diploid vs polyploids in natural habitats suggests that the polyploids are more prevalent on account of broader ecological tolerances and invasive nature—see further discussion by Lavania [34]. Levin [42] argues that under disturbed environmental conditions speciation primarily would involve mechanisms that produce reproductively isolated lineages. As such polyploid species may themselves spawn additional higher level polyploids either through crosses with diploid species or between pre-existing polyploids. He further emphasized that the mean increase in chromosome number diversity per lineage per million years in herbaceous plants is five times that of shrubs and 50 times that of trees, calling for a genetic basis for the proportional increase in herbaceous species expected to occur over the coming centuries.

Levin [42] has proposed that the percentage of polyploid species is likely to exceed by 50% within the next 500 years vs. 35% today; and that most polyploid species shall be mainly herbaceous plants. It is further suggested that most of the polyploid herbs thus emerging shall be perennial ones owing to their higher adaptability to environmental changes [53] which are more adaptable to environmental changes.

Levin [42], Gao [22] identify five main types of plant speciation. Autopolyploid speciation is the dominant type in the context of climate change, followed by allopolyploid speciation, whereas speciation due to chromosomal rearrangements, homoploid hybrid speciation and lineage splitting are not pervasive. More specific details are provided in the articles cited above.

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References

1. Abraham A. Chromosome constitution and oil content in the coconut endosperm. *J Indian Bot Soc.* 1963;42A:1–3.
2. Abraham A, Mathew PM. Cytology of coconut endosperm. *Ann Bot.* 1963;27:505–12. <https://doi.org/10.1093/oxfordjournals.aob.a083866>.
3. Abraham A, Ninan CA, Gopinath P. Cytology of development of abnormal endosperm in Philippine Makapuno coconuts. *Caryologia.* 1965;18:395–408. <https://doi.org/10.1080/00087114.1965.10796182>.
4. Banerjee M, Sharma AK. Variations in DNA content. *Experientia.* 2020;35:42–3. <https://doi.org/10.1007/BF01917865>.
5. Bansal YK, Sen S. Multi-stranded chromosomes in the differentiated tissue of *Hordeum vulgare*. *Cytologia.* 1983;48:403–5. <https://doi.org/10.1508/cytologia.48.403>.
6. Bassi P. Quantitative variations of nuclear DNA during plant development: a critical analysis. *Biol Rev.* 1990;65:185–225. <https://doi.org/10.1111/j.1469-185X.1990.tb01424.x>.
7. Bayliss MW. Chromosomal variation in plant tissues culture. *Int Rev Cytol.* 1980;1980(Suppl. 11a):113–44.
8. Bennett MD. Natural variation in nuclear characters of meristems in *Vicia faba*. *Chromosoma.* 1970;29:317–35. <https://doi.org/10.1007/BF00325946>.
9. Bennett MD, Rees H. Induced and developmental variation in chromosomes of meristematic cells. *Chromosoma.* 1969;27:226–44. <https://doi.org/10.1007/BF00326147>.
10. Bennett MD, Smith JB, Smith D. The Mitotic cycle duration in *Vicia Faba* root-tip meristems with different sized chromosomes. *Caryologia.* 1972;25:445–53. <https://doi.org/10.1080/00087114.1972.10796498>.
11. Bomfleur B, McLoughlin S, Vajda V. Fossilized nuclei and chromosomes reveal 180 million years of genomic stasis in royal ferns. *Science.* 2017;343:1376–7. <https://doi.org/10.1126/science.1249884>.
12. Bonde SD, Varghese KKP, Shindikar MR, Gamre PG. Fossil chromosomes in an extinct Gondwanan seed plant (*Pentoxylon*). *Curr Sci.* 2004;87:865–6.

13. Cai L, Xi Z, Amorim AM, Sugumaran M, Rest JS, Liu L, Davis CC. Widespread ancient whole-genome duplications in Malpighiales coincide with Eocene global climatic upheaval. *New Phytol*. 2019;221:565–76. <https://doi.org/10.1111/nph.15357>.
14. Carrano A, Thompson L, Lindl P, et al. Sister chromatid exchange as an indicator of mutagenesis. *Nature*. 1978;271:551–3. <https://doi.org/10.1038/271551a0>.
15. Carnevali GMZ. Plant polytene chromosomes. *Genet Mol Biol*. 2000;23:1043–50.
16. D'Amato F. Role of polyploid in reproductive organs and tissues. In: Johri BM, editor. *Embryology of angiosperms*. Berlin: Springer; 1984. p. 519–66.
17. D'Amato F. Polyploidy in cell differentiation. *Caryologia*. 1989;42:183–211.
18. Edgar BA, Zielke N, Gutierrez C. Endocycles: a recurrent evolutionary innovation for post-mitotic cell growth. *Nat Rev Mol Cell Biol*. 2014;15:197–210. <https://doi.org/10.1038/nrm3756>. PMID:24556841 Review.
19. Evans LS, Van't HJ. Is polyploidy necessary for tissue differentiation in higher plants? *Am J Bot*. 1975;62:1060–4. <https://doi.org/10.1002/j.1537-2197.1975.tb11770.x>.
20. Fawcett JA, Maere S, Van De Peer Y. Plants with double genomes might have had a better chance to survive the Cretaceous-Tertiary extinction event. *Proc Natl Acad Sci*. 2009;106:5737–42.
21. Fussell CP. Telomere associations in interphase nuclei of *Allium cepa* demonstrated by C-banding. *Exp Cell Res*. 1977;110:111–7.
22. Gao J. Dominant plant speciation types. A commentary on: 'Plant speciation in the age of climate change. *Ann Bot*. 2019;124:iv–vi. <https://doi.org/10.1093/aob/mcz174>.
23. Gerstel DU. Phenotypic and chromosomal abnormalities associated with the introduction of heterochromatin from *Nicotiana glauca* into *N. tabacum*. *Genetics*. 1967;56:483–502. <https://doi.org/10.1093/genetics/56.3.483>.
24. Gerstel DU, Burns JA. Enlarged euchromatic chromosomes ('megachromosomes') in hybrids between *Nicotiana tabacum* and *N. plumbaginifolia*. *Genetica*. 1976;46:139–53. <https://doi.org/10.1007/BF00121030>.
25. Gotoh E, Durante M. Chromosome condensation outside of mitosis: mechanisms and new tools. *J Cell Physiol*. 2006;209:297–304.
26. Holmes BE, Mee LK, Hornsey S, Gray LH. The nucleic acid content of cells in the meristematic elongating and fully elongated segments of roots of *Vicia faba*. *Exp Cell Res*. 1955;8:101–13. [https://doi.org/10.1016/0014-4827\(55\)90046-X](https://doi.org/10.1016/0014-4827(55)90046-X).
27. Innocenti AM. Cyclic Changes of Histones/DNA ratio in differentiating nuclei of metaxylem cell line in *Allium Cepa* root tip. *Caryologia*. 1975;28:225–8. <https://doi.org/10.1080/00087114.1975.10796612>.
28. Innocenti AM, Avanzi S. Some cytological aspects of the differentiation of metaxylem in the root of *Allium Cepa*. *Caryologia*. 1971;24:283–92. <https://doi.org/10.1080/00087114.1971.10796436>.
29. Jiao Y, Wickett N, Ayyampalayam S, et al. Ancestral polyploidy in seed plants and angiosperms. *Nature*. 2011;473:97–100. <https://doi.org/10.1038/nature09916>.
30. Joachimiak A, Przywara L, Ilnicki T, Kowalska A. Megachromosomes in tissue culture of *Allium*. *Genetica*. 1993;90:35–40.
31. Jones N. New species with B chromosomes discovered since 1980. *Nucleus*. 2017;60:263–81. <https://doi.org/10.1007/s13237-017-0215-6>.
32. Kereso J, Praznovszky T, Cserpan I, Fodor K, Katona R, et al. De novo chromosome formations by large-scale amplification of the centromeric region of mouse chromosomes. *Chromosome Res*. 1996;4:226–39.
33. Lavania UC. Polyploidy, body size, and opportunities for genetic enhancement and fixation of heterozygosity in plants. *Nucleus*. 2013;56:1–6. <https://doi.org/10.1007/s13237-013-0075-7>.
34. Lavania UC. Plant speciation and polyploidy: in habitat divergence and environmental perspective. *Nucleus*. 2020;63:1–5. <https://doi.org/10.1007/s13237-020-00311-6>.
35. Lavania UC, Basu S, Kushwaha JS, Lavania S. Seasonal temperature variations influence tapetum mitosis patterns associated with reproductive fitness. *Genome*. 2014;57:517–21. <https://doi.org/10.1139/gen-2014-0092>.
36. Lavania UC, Sharma AK. Centromeric ring and arrangement of centromeres in interphase of *Lathyrus sphaericus* as detected by C-banding. *Cytologia*. 1984;49:745–9. <https://doi.org/10.1508/cytologia.49.745>.
37. Lavania UC, Sharma AK. Arrangement of the Interphase chromosomes in the nucleus. *J Hered*. 1985;76:395–6. <https://doi.org/10.1093/oxfordjournals.jhered.a110125>.
38. Lavania UC, Srivastava S. Ploidy dependence of chromosomal variation in callus cultures of *Hyoscyamus muticus* L. *Protoplasma*. 1988;145:55–8.
39. Lavania UC, Srivastava S. Evolutionary genomic change paralleled by differential responses of 2x and 4x calli cultures. *Experientia*. 1990;46:322–4.
40. Lavania UC, Srivastava S, Lavania S. Ploidy mediated reduced segregation facilitates fixation of heterozygosity in the aromatic grass, *Cymbopogon martini* (Roxb.). *J Hered*. 2010;101:119–23.
41. Lavania UC, Srivastava S, Basu S, Misra NK, Mukai Y. Autopolyploidy differentially influences body size in plants, but facilitates enhanced accumulation of secondary metabolites, causing increased cytosine methylation. *Plant J*. 2012;71:539–49.
42. Levin DA. Plant speciation in the age of climate change. *Ann Bot*. 2019;124:769–75. <https://doi.org/10.1093/aob/mcz108>.
43. Liu X, Chen Z, Shi X. The B Chromosome: an optimum platform for maize minichromosome engineering. *Crit Rev Plant Sci*. 2024;13:1–6. <https://doi.org/10.1080/07352689.2024.2427550>.
44. Lyndon RF. The nucleus—its structure, function and development. In: Pridham JB, editor. *Plant cell organelles*. Academic Press Ltd.; 1968.
45. McClintock B. The production of homozygous deficient tissues with mutant characteristics by means of the aberrant mitotic behavior of ring-shaped chromosomes. *Genetics*. 1938;23:315–76.
46. Mitchell JP, van der Ploeg R. Nuclear changes accompanying cell differentiation in stems of *Pisum sativum* L. *Histochemistry*. 2018;75:327–40. <https://doi.org/10.1007/BF00496736>.
47. Murray AW. How to compact DNA. *Science*. 1998;282:425–7.
48. Nagl W. DNA reduplication and polyteny understood as evolutionary strategies. *Nature*. 1976;261:614–5.
49. Nagl W. Polytene chromosomes of plants. *Int Rev Cytol*. 1981;73:21–53.
50. Nagl W, Pohl J, Radler A. The DNA endoreduplication cycles. In: Bryant JA, Francis D, editors. *The cell division cycle in plant*. Cambridge: University Press; 1985. p. 217–32.
51. Niwa O, Matsumoto T, Chikashige Y, Yanagida M. Characterization of *Schizosaccharomyces pombe* minichromosome deletion derivatives and a functional allocation of their centromere. *EMBO J*. 1989;8:3045–52.
52. Perry P, Wolff S. New Giemsa method for the differential staining of sister chromatids. *Nature*. 1974;251:156–8.
53. Rice A, Šmarda P, Novosolov M, Drori M, Glick L, Sabath N, Meiri S, Belmaker J, Mayrose I. The global biogeography of polyploid plants. *Nat Ecol Evol*. 2019;3:265–73.
54. Riley R. Cytogenetics of chromosome pairing in wheat. *Genetics*. 1974;78:193–203. <https://doi.org/10.1093/genetics/78.1.193>.
55. Riley R, Chapman V. Genetic control of the cytologically diploid behaviour of hexaploid wheat. *Nature*. 1958;182:713–5.

56. Schubert I. Some past developments and open questions in understanding the biology of nucleus. *Nucleus*. 2017;60:247–9. <https://doi.org/10.1007/s13237-017-0217-4>.
57. Schubert I, Oud JL. There is an upper limit of chromosome size for normal development of an organism. *Cell*. 1997;88:515–20.
58. Schvartzman JB, Cortés F. Sister chromatid exchanges in *Allium cepa*. *Chromosoma*. 1977;62:119–31. <https://doi.org/10.1007/BF00292634>.
59. Sharma AK. A new concept of speciation in plants. *Caryologia*. 1956;9:93–130.
60. Sharma AK. Change in chromosome concept. *Proc Indian Acad Sci*. 1978;87B:161–90.
61. Sharma AK, Aiyangar HR. Occurrence of B-chromosomes in diploid *Allium stracheyi* Baker and their elimination in polyploids. *Chromosoma*. 1961;12:310–7. <https://doi.org/10.1007/BF00328926>.
62. Sharma AK, Sharma A. Fixity in chromosome number of plants. *Nature*. 1956;177:335–6. <https://doi.org/10.1038/177335a0>.
63. Sharma AK, Sharma A. Chromosomal alterations in relation to speciation. *Bot Rev*. 1959;25:514–44.
64. Sperling K, Rao PN. The phenomenon of premature chromosome condensation: its relevance to basic and applied research. *Hum Genet*. 1974;23:235–58. <https://doi.org/10.1007/BF00272508>.
65. Storey WB. Somatic reduction in cycads. *Science*. 1968;159:648–50. <https://doi.org/10.1126/science.159.3815.648>.
66. Tourdot E, Grob S. Three-dimensional chromatin architecture in plants. *Eur J Cell Biol*. 2023;102: 151344. <https://doi.org/10.1016/j.ejcb.2023.151344>.
67. Taylor JH. Sister chromatid exchanges in tritium labeled chromosomes. *Genetics*. 1958;43:515–29.
68. Taylor JH, Woods PS, Hughes WL. The organization and duplication of chromosomes as revealed by autoradiographic studies using tritium-labeled thymidine. *Proc Natl Acad Sci USA*. 1957;43:122–8.
69. Tjio JH, Levan A. The chromosome number of man. *Hereditas*. 1956;42:1–6. <https://doi.org/10.1111/j.1601-5223.1956.tb03010.x>.
70. Vimala Y, Lavania S, Lavania UC. Chromosome change and karyotype differentiation—implications in speciation and plant systematics. *Nucleus*. 2021;64:33–54. <https://doi.org/10.1007/s13237-020-00343-y>.
71. Vimala Y, Lavania UC. Genomic territories in inter-genomic hybrids: the winners and losers with hybrid fixation. *Nucleus*. 2021;64:1–6. <https://doi.org/10.1007/s13237-021-00348-1>.
72. Vishnu-Mittre S. Nuclei and chromosomes in fossil fern. In: Darlington CD, Levis KR, editors. *Chromosomes today*, vol. 2. Edinburgh: Oliver and Boyd Ltd; 1969. p. 250–1.
73. Wagenaar EB. End-to-end chromosome attachments in mitotic interphase and their possible significance to meiotic chromosome pairing. *Chromosoma*. 1969;26:410–26.
74. Waldeyer W. Ueber Karyokinese und ihre Beziehungen zu den Befruchtungsvorgängen. *Arch Mikr Anat*. 1888;32:1–122.
75. Watson JD, Crick FHC. Molecular structure of nucleic acids: a structure for deoxyribose nucleic acid. *Nature*. 1953;171:737–8.
76. Wendel JF. The wondrous cycles of polyploidy in plants. *Am J Bot*. 2015;102:1753–6. <https://doi.org/10.3732/ajb.1500320>.
77. Winge Ö. The chromosomes. Their numbers and general importance. *Carlsberg Lab Copenhagen CR trav*. 1917;13:131–75.
78. Winkler H. Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. *Zeitschrift für Botanik*. 1916;8:417–531.

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