B CHROMOSOMES IN ANGIOSPERM – A REVIEW

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A review article on B chromosomes (Bs) in angiosperms is documented considering occurrence, morphology, polymorphic B forms, divisional phase heterogeneity, chromatin organization and gene content, sequence composition, origin, evolutionary aspects and significant role on host with an objective to foresee the evolutionary perspectives as it still remains an enigma. Irrespective of the origin of Bs, it seems that they have attained the following modifications, namely, insertion of centromeric and telomeric sequences, structural reorganization and procuring mitotic and meiotic drives but shows genetic inertness and present in the host as selfish DNA. In the context, few questions are raised. Further, scientific quest may unravel the unexplored information about Bs to ascertain its evolutionary perspectives, if any.

***Key words**: distribution, morphology, polymorphism, mitotic and meiotic drives, sequence analyses, origin and evolution.*

Introduction. B chromosomes (Bs) are defined as additional dispensable components of the genome which exhibit characteristic non-Mendelian and irregular pattern of inheritance and do not pair or recombine with any of the diploid set of A-chromosome during meiosis. Randolph [1] first coined the term 'B chromosomes' in maize. Bs were firstly identified in the leaf-footed plant bug insect *Metapodius*, now known as *Acanthocephal* [2] and in coleopteran insects *Diabrotica soror* and *D. punctata* [3] as supernumerary chromosomes. In plant species, the pioneer reports of Bs were in rye (*Secale cereale*, $2n = 2x = 14$+Bs [4]) and maize (*Zea mays*, $2n = 2x = 20$+Bs [5]) as extra chromosomal fragments (K chromosomes different from A sets). Bs are also referred to as supernumerary or accessory chromosomes in maize by Longley [6].

Definitional simplicity of Bs does not accord with the complexity of diverse range of B chromosome system found in plant species such as 1) non-random distribution of novel B element among major groups of angiosperm lineages and among lineages within families [7]; 2) prevalently reported to be genetically inert but molecular analyses reveal the presence of rich gene derived sequences [8]; 3) negative (detrimental to fertility [9]) as well as positive (adaptive significance in *Allium schoenoprasum* [10, 11], crown rust resistance in *Avena sativa* [12]) phenotypic expression; 4) mitotic and meiotic drive processes; 5) complexity regarding its origin [13–16].

The present review article encompasses the significant findings on B chromosomes in angiosperm in a comprehensive manner on the basis of occurrence, morphology, divisional phase heterogeneity, chromatin organization and gene content, sequence composition, origin, polymorphic B forms evolutionary aspects and significant role on host of B-chromosomes with an objective to foresee the evolutionary perspectives. The authors hope that the present article may provide insight for further exploration of Bs in unravelling the mystery associated to it.

Occurrence. Levin et al. [7] reported representation of B elements in 8.0 % monocots and 3.0 % eudicots (4.1 % of angiosperm) with significant heterogeneity in frequency at orders, families and generic level, with many hot spots in Liliales and Commelinales. Disparity in the frequency of B chromosomes at genus and species level is reported as the possible outcome of variation in genome size [17, 18], breeding system [19] and basic number of A chromosomes [18]. Frequency of B chromosomes is reported up to 34 in maize (involving 15.5 % increase in nuclear DNA content [20]), 20 in *Allium schoenoprasum* [21], not more than 3 in *Lolium perenne* [20] and *Brachycome dichromosomatica* [22], among others.

Palestis et al. [23] assessing B chromosome frequency across species in angiosperm suggested that Bs are more likely to occur in outcrossing than in inbred species, and their presence is also positively correlated with genome size and negatively with chromosome number. Levin et al. [7] opined that angiosperm species with very small genomes lack B-elements. Species possessing larger amount of noncoding DNA possibly contributes more B chromosomes [9, 24] or provide force for triggering the formation of B-elements [7].

Trivers et al. [18] demonstrated that polyploidy in angiosperms had no positive effect on the presence of Bs rather had slight negative effect. No correlation between polyploids and Bs has been attributed to 1) loss of noncoding DNA [25], 2) doubling of chromosome number eliminates Bs [18], 3) apomictic mode of reproduction in polyploids [26], 4) negative correlation between DNA content per diploid genome and polyploids [27] and among others.

It seems that B chromosomes lacking a definite mode of distribution are non-randomly reported among angiosperm members.

Morphology. The structure and organization of B chromosomes are studied in relation to standard normal (A chromosomes) in mitotic metaphase cells apart from obtaining useful information from somatic interphase cells where they are represented as chromocentres (*Zea mays* [28], *Picea glauca* [29], *Rosa rugosa* [30]). Karyotype analysis reveals distinctiveness of B elements from A set in size and centromeric position [13].

B chromosomes exist either as isochromosomes (*Crepis capillaris* [31]) or with subterminal centromere or as frequent telocentrics (*Hypochoeris maculate* [32]). In general, B chromosomes are smaller than A chromosomes. Jones [13] estimated about 40 % of angiosperm taxa possessing B elements having the size of 1/4 to 3/4 of the average of As and 26 % showing B-size less than the smallest A. Among the remaining 1/3 species, B elements are categorized as very small micros (*Campanula rotundifolia* [33], *Linanthus pachyphyllus* [34]). In some taxa Bs are equal to and indistinguishable from the As at mitosis (*Clarkia elegans* [35], *Sorghum nitidum* [36], *Erianthus munja* [37]). 'Large' B chromosomes are also reported in flowering taxa (*Rumex thyrsiflorus* [38], *Calycadenia oppositifolia* and *C. ciliosa* [39], *Plantago serraria* [40]). Tian and Li [41] reported *in vitro* (callus derived from immature embryo) variation (0 to 4 in 40 days old callus) of Bs in 65.6 % cells of *Triticum aestivum* and *Secale cereale*.

Polymorphic B forms. Reports of polymorphism, both structural and numerical, are frequent among B containing species. Two or more polymorphic forms reported in a species are like metacentric and telocentric in *Aegilops mutica* [42] or the large and the micro-sized ones in *Brachycome dichromosomatica* [43]. Loidl [44] differentiated three sizes of Bs in *Allium flavum* by overall size and arm ratio using Giemsa C-banding. In *Allium schoenoprasum*, a total of 29 different B-karyotype consisting various sizes of telocentric and metacentric forms are documented [45]. About 29 polymorphic B forms differing in terms of length, centromeric position and heterochromatin content are noted in the genus *Aster* comprising of 2 species, 4 subspecies and 6 variants [46–52]. Bs are found to vary in number among (and within) individuals of a species (*Picea glauca* – $2n$ = 24As+0–6Bs, *Zea mays* – $2n$ = 20As+0–34Bs [8]).

The origin of B polymorphic forms has been ascribed due to 1) centromeric misdivision of single unpaired chromosome at meiosis resulting to the formation of isochromosome and other derivatives through deletion of arms [13]; 2) outcome of a dynamic system involving continuous arm racing between A and B chromosomes [8]; 3) ephemeral product of the consequences of heritable chromosomal mutation within population [53–55].

Frequent structural and numerical variations noted among B containing species possibly reflects that they do not possess any constrain upon the cellular structure and organization as do the A-chromosome type.

Divisional phase heterogeneity. *Mitosis*. About 1/3 of the B-containing species exhibit mitotic conserveness [9, 13]. Mitotic stability of Bs in the sporophyte seems to be common among grasses apart from scanty reports of non-disjunction during the first zygotic division and in endosperms [56]. Mitotic conserveness of Bs is rather rare in *Allium* spp. [13]. In *Brachycome dichromosomatica*, macrotype B is stable but microforms are numerically variable [57]. Sectoral mitotic instability within a species results in selective elimination of B element from roots in *Erianthus munja* and *E. ravennae* [37], stem and leaves of *Sorghum stipoideum* [58] and adventitious roots of *Agropyron mongolicum* [59].

Apart from sporophyte, normal mitotic behavioural deviation of B elements is well studied from the first and the second mitosis of microgametogenesis significant for post mitotic drive in maize [60, 61], rye [62] among others. Non-disjunction mediated aberrant mitotic drive of rye and maize differs between plant types depending on the stage of occurrence. Non-disjunction in rye involves the following: 1) occurs at first mitosis of both microspore [62] and megaspore [63]; 2) is governed by adhesion site on either side of centromere which prevents the sister chromatid separation at anaphase after normal centromeric division [64]; 3) factor mediating non-disjunction is located at the end of long arm of B [65]; 4) is controlled by trans-acting element/gene located in the distal half of the long arm of standard B [66]; 5) specific sequences belonging to two families, E3900 and D1100 are reported as controlling elements [67], and comprises of repeats which are also A genome representative [68–71] and are transcriptionally active in anthers [8]. Mitotic drive based on non-disjunction of B element in rye is strong enough to overcome a negative selection force acting against Bs accumulation [72], enforcing stability and uniformity in a given population.

Non-disjunction-mediated mitotic drive in maize involves the following: 1) is restricted only to the second pollen mitosis [60, 73], 2) A chromosomes control preferential fertilization of egg by the B-carrying sperm, 3) is controlled by sticking site in the centromeric heterochromatin [61, 74, 75]; 4) four B segments namely, euchromatin tip, proximal euchromatin, centric heterochromatin or B-knob and minute short arm are regulating factors [13] for mechanising mitotic drive. The minute arm retains the ability for controlling the rate of non-disjunction. Jones [13] opined that centromeric adhesive site controlling non-disjunction of Bs acts as cis-acting receptor. Lamb et al. [76] reported that the euchromatin tip and proximal euchromatin block serve as trans-acting regulatory element on centromeric adhesive site. A small fraction of B specific ZinB sequence, nearly 700 kb domain, is identified to interact with centromeric histone H_3 variant (CENH3) providing the function of centromere [77].

Rye and maize models suggest that non-disjunction mediated mitotic drive of Bs in gametes and somatic cells

in a selfish way try to enhance their transmission potential with high degree of autonomy and genetic sophistication.

Meiosis. Meiotic behavioural pattern of B elements is rather variable among species containing Bs excepting for the universality of non-pairing and recombination with A set [13, 14, 20, 67]. In rare cases A-B translocation is reported (e.g. rye [78]) resulting into divorce of B element from rest of the genome by meiotic isolation [67]. Pairing and recombinational isolation of B chromosome in relation to A set may possibly be due to 1) size differences [13], 2) epigenetic and replicational variations [79, 80], 3) presence of B specific sequence as in rye [71], 4) nuclear disposition of Bs [9, 14], 5) selection biasness during synaptonemal complex formation [81] and among others.

Meiotic behaviour and its associated consequences of B chromosomes have been found to follow either of the types: 1) two or higher number of B element homologous to one another shares many possibilities of pairing arrangements from bivalent to multivalent formation, 2) unpaired Bs possesses the capacity to pass through meiosis as univalents, 3) B elements solely present as univalent and 4) non-pairing Bs coupled with meiotic drive. Presence of 2 Bs often involves in inter-arm as well as interchromosome pairing [82]. Involvement of 2 Bs forming normal bivalent is also reported, which results into near identical A-chromosome meiotic behaviour and stable segregation [9]. Pairing nature of B forms consisting standard Bs (stB), deficient B (dB) and B isochromosome (iso-B) has been extensively analysed in terms of synaptonemal complex (sc) formation [81].

Few observations highlighted in *Crepis* spp. Regarding meiotic behaviours of Bs are 1) multivalent formation of 4Bs during zygotene and pachytene [31], 2) 4B forms quadrivalent composed of partially synapsed Bs with long arm of A chromosome complement named as K10 [81], 3) tend to have a peripheral location in nucleus with delayed pairing compared to As [83], 4) stB and dB together formed homologous as well as non-homologous synapsis devoid of any axial equalization, and is only observed in 9.5 % cells of metaphase I (MI), often undergoing pairing competition among dB with 2 stB [13]. Jones [13] assessed the characteristic features of pachytene pairing of iso-Bs and they are 1) peripheral positioning, 2) delayed pairing, 3) formation of mostly hairpin loop structure, 4) terminal or centromeric synapsis or both and 5) predominance of self-synapsed short arm iso-B univalent. Santos et al. [84] also studied various pairing combination of short and long arm iso-Bs together with stB in *Crepis*. In many plant species non-pairing of Bs during meiosis resulting in univalent formation has been reported which is not a hindrance to their existence in population [9]. Univalent B commonly undergoes fold back pairing to form hairpin loop structure in *Crepis capillaries* [85] or undergoes self synapsis at pachytene [86]. Carlson and Roseman [87] identified two distinct regions of B element suppressing meiotic loss when unpaired that allows univalent B-migration individually to any of the poles of anaphase I (AI) following division at anaphase II (AII) with minimal or no loss. Jones [13, 82] reported various mechanisms minimizing mitotic and meiotic B chromosome loss for achieving population equilibrium. González-Sánchez et al. [88] identified one A located factor, seemed to be codeterminant of repressing meiotic loss of Bs.

B chromosomes show variable meiotic behaviour and segregation distortion and consequently do not confirm to Mendelian pattern of inheritance. Accumulation of B chromosomes takes place before, during or after meiosis and such collection of B elements signify parasitic property [14]. Results of B element transmission analysis specifically in rye reveal that meiotic drive may be autonomous and at the same time be the subject to genetic control by their host signifying selection and evolutionary forces [13]. It seems that meiotic drive is an important regulatory factor for maintaining B polymorphism even against the gradient of negative phenotypic effect.

Post-meiotic drive. B elements in some cases gain heritable advantage in transmission higher than Mendelian expectations [13]. Post-meiotic drive is rather common in flowering plants [8] and directed by non-disjunction which occurs in 1) gametophytic phase (common in Gramineae [67]), 2) the first pollen mitosis as well as the first egg cell mitosis (e.g. rye [8, 89]), 3) the second pollen mitosis (e.g. maize [20, 67]) and among others. In *Allium cernuum*, Bs drift to the poles at AI with minimal loss and are driven to AII with limited elimination [90]. Similar cellular locomotion of Bs at microsporogenesis was also studied in *Plantago serraria* [40]. Fröst [91] earlier reported considerable loss of unpaired Bs in *Centaurea scabiosa* at AII. In *Lolium callosum* the univalent Bs of egg mother cells lying at micropylar end during meiosis passes into the egg with 80 % success rate [92]. Jones et al. [67] reported that in *Lilium callosum* B transmission through the pollen is normal/Mendelian whereas in female meiosis it is based on spindle asymmetry. Apart from the citations mentioned, there are plant species (e.g. *Poa alpine* [93], *P. trivialis* [94], *Centaurea scabiosa* [95], *Ranunculus acris* [96], *Allium schoenoprasum* [45], *Guizotia scabra* [97]) where all B chromosomes do not show any definite mode of transmission.

Differential mitotic as well as meiotic behavioural pattern of B element hypothecated by several drifting mechanisms serves as compensating drive against the possible elimination of the non-essential chromosome type in the course of evolution maintaining its species level distributional potentiality.

Chromatin organization and gene content. Chromatin organization in B elements shows considerable variability among plant species, even at the intraspecific level, in relation to heterochromatic content [13]. Chromatin status of Bs in different species has been analysed either using chromocenter staining technique [98] or by Giemsa banding of c-metaphase [99–101]. Cai and Chinnappa

[101] reported that most of the length of Bs in *Allium cernuum* shows C-bands but Friebe [102] opined that C-bands are restricted only at telomere. Vosa [99] observed that B elements are completely euchromatic in nature in *Allium flavum* in contrast to the observation made by Loidl [44], who reported the presence of small terminal and interstitial C-bands. Greihuber and Speta [98] documented that Bs are less heterochromatic than As in *Scilla vvedenskyi*; while in *Ranunculus ficaria*, C-banding is reported to be distributed on nearly entire B length with none to be visualised on A chromosome [100]. Jones [13] noted 3 distinct classes of heterochromatin blocks in maize B system, and they are positioned in B centromere, distal part of B long arm and small single knob adjacent to B centromere. The knob heterochromatin of maize B element provides sticking site for non-disjunction during second pollen mitosis and also reported to be acting as last component of genome to complete DNA replication [103].

Genetic organization of B elements in rye, maize among others is the regulatory factor for their own transmission properties [13]. Genes localized on Bs are derived from As, and the B elements possibly degenerated and silenced via Muller's Ratchet mechanism [104]. Lynch and Conery [105] estimated half life of active duplicated genes undergoing mutation, silencing and loss in 2–7 million years. Houben et al. [8] shows the possibility of few B located gene(s) may still be in active form depending on the age of a B element. Furthermore, the authors opined that B-located active genes share extra-copies in the genome but strikingly not associated with more severe phenotypic changes. Non-correlation between gene copy number and phenotypic intensity has possibly been mediated by dosage compensation mechanisms, which differ among taxa involving recruitment of chromatin regulatory complex to regulate gene expression [106]. Houben et al. [8] also hypothesized that A-derived proto B genes may possibly be down-regulated by dosage compensation.

B chromosome carries ribosomal genes [104, 107] though reported to be mostly inactivate [108]. *In situ* hybridization of B chromosome with biotin-labelled probe detects about 400 copies of rRNA cistrons localized at each telomere of B element in *Crepis capillaris* [109]. Donald et al. [110] using FISH technique identified rRNA gene cluster in *C. capillaris* located at the satellite end of metacentric B. The rDNA of large B in *Brachycome dichromosomatica* is found transcriptionally inactive following the study involving Reverse Transcriptase Polymerase Chain Reaction (RT-PCR) using 40S rRNA precursors [8]. Leach et al. [111] reported Bs with active Nucleolar Organizing Region (NOR) genes with reduced level of transcriptional activity. Flavell and Rimpau [112] estimated that about 650 rRNA genes are present in each rye B-chromosomes. Niwa and Tsujmoto [113] reported lack of 18S – 26S rRNA gene fractions in rye B. Using probed pTa71 and pTa794 corresponding to 25S – 5.8S – 18S (NOR) and 5S rDNA multigene family, no signal could be detected from Bs of Portuguese strain of rye [114]. Martis et al. [15] identified 4000 putative gene sequences in rye B chromosomes.

Sequence composition. Sequence analysis of Bs following the application of molecular tools reveals the abundance of various classes of repeats. In rye system, the repeat sequences reported are 1) one 1.1 kb [68] and 3.9 kb repeats [69] and both localized in the distal region of long arm of B element [13] and 2) pSc74 and pSc119.2 repeats, reported in As are persistently present in B-telomeric region [114] and also in interstitial site of Bs [115].

In maize system, the repeat sequences and their functions are 1) 185 bp repeats in $1.25 \cdot 10^4$ copies positioned on the small heterochromatic knob of B chromosome [116], and 184 and 185 bp repeats with high homology between them [117]. The repeat sequences are localized both in centromeric heterochromatic knob of B as well as in As [117], 2) the 700 kb centromeric domain of maize B chromosome contains an array of three repeat sequences namely, B specific repeat – ZmBs, 156 bp satellite repeat – Cent C and centromere specific retrotransposon – CRM element [118–121]; 3) the 9 Mb of ZmBs repeats represented in the functional region of Bs possessing strong correlation between retained size and meiotic transmission [122]; 4) 55 kb size of ZmBs neighbouring to 37 kb large DNA fragment is crucial for meiotic transmission [9, 123]; 5) CentC and CRM are also reported as key elements of maize centromere [121] embedded within larger matrix array of ZmBs repeat [77], which is essential for proper kinetochore formation [124, 125]; 6) CENH3 is found to be associated only with CentC rich domain of maize B centromere [121] showing strong correlation with the domain size and chromosome stability [77].

In *Brachycome dichromosomatica* B specific 176 bp tandem repeat sequence has been identified [126]. Jones [13] reported that sequencing and quantitative estimation of diploid genome of the species reveals $1.8 \cdot 10^5$ copies of six individual repeats with single macro B.

Sequence analysis of B elements in plant species documents predominance of several classes of repeating blocks, some of which are specific to Bs while the rest share the common platform with As. Distinctiveness in chromatin condensation and heterochromatin composition, presence of wide array of both specific and non-specific repeating sequences, gene derived sequences and multicopy rDNA and NOR genes possibly contributes to the isolation of B elements from A genome fraction. Such distinctiveness of Bs possibly provides autonomy in the form of specialized cell division and inheritance mode.

Origin. Conventional and widely accepted thought is that B chromosomes are the derivatives of As [20], which has been experimentally explained using molecular tools in *Crepis capillaris* [127], *Zea mays* [77, 128], rye [129], among others. Documented reports of B origin from As

are 1) as small centric fragment due to unequal translocation and chromosome number reduction in *Crepis fuliginosa* ($2n = 8 + Bs$) during its evolution from *C. neglecta* ($2n = 6$) [20, 67]; 2) spontaneous generation of Bs in response to new genomic condition following interspecific hybridization in *Coix aquaticus* and *C. gigantea* [130]; 3) allopolyploidization induced chromosomal rearrangement coupled with selective elimination, reorganization and preferential sequence amplification [131]; 4) agglome-ration of tandem repeat sequence of As through more than a single excision subsequently followed by addition of extra-chromosomal circular DNA (eccDNA) and centric as well as telomeric sequence in *Brachycome dichromosomatica*, *Zea mays* and *Secale cereale* [67, 129, 132, 133]; 5) through recombination of several A chromosomes in maize followed by capturing of additional A-derived and organelle sequences and subsequent amplification [15], and possibly among others.

Houben et al. [134] opined that supernumerary A segments serve as B founder sequences but the source of centromeric sequences is still to be a mystery. Rare *de novo* formation of centromere is reported to be possible [135].

NOR comprising clusters of rRNA repeats are reported to be prone to chromosome breakage providing detachment site through which Bs can be generated [14]. Bs are thought to be accumulated in *Plantago lagopus* following series of events starting from massive amplification of 5S rDNA to release of the amplified segments and *de novo* addition of telomere [136], and stabilization by obtaining preferential transmission novelty [67]. McGrath and Helgeson [137] hypothesized that species specific difference in rDNA condensation might have led to the formation of neoB chromosomes in somatic hybrid raised between *Solanum brevidens* and *S. tuberosum*. The genus *Brachycome* also possesses different degree of rDNA condensation resulting in generation of various rDNA containing B elements [14, 97]. Amalgamation of transposable DNA from various sources is also predicted for the origin of B element in few taxa [107].

Cytomixis (mixing of cytoplasm in somatic and reproductive cells through cellular bridging, thereby forming a syncytia involving 2 to many cells [138]) resulting in fragmentation of A chromosomes is reported to be the mechanism for the origin of Bs [139]. Yanyou and Jiemei [140] put forward the supposition of cytomixis for the origin of B chromosomes. Sheidai [141] also suggested that B chromosomes pioneered cytomixis possibly played a significant role in the evolution of plant species. Minute fragments of variable numbers (1 to 5) and sizes (0.04 to 0.09 μm) with possible constrictions are referred to as Bs-like structure in a stress cytomictic population of *Corchorus fascicularis* [138]. These results signify the potentiality of the origin Bs from As during cytomixis.

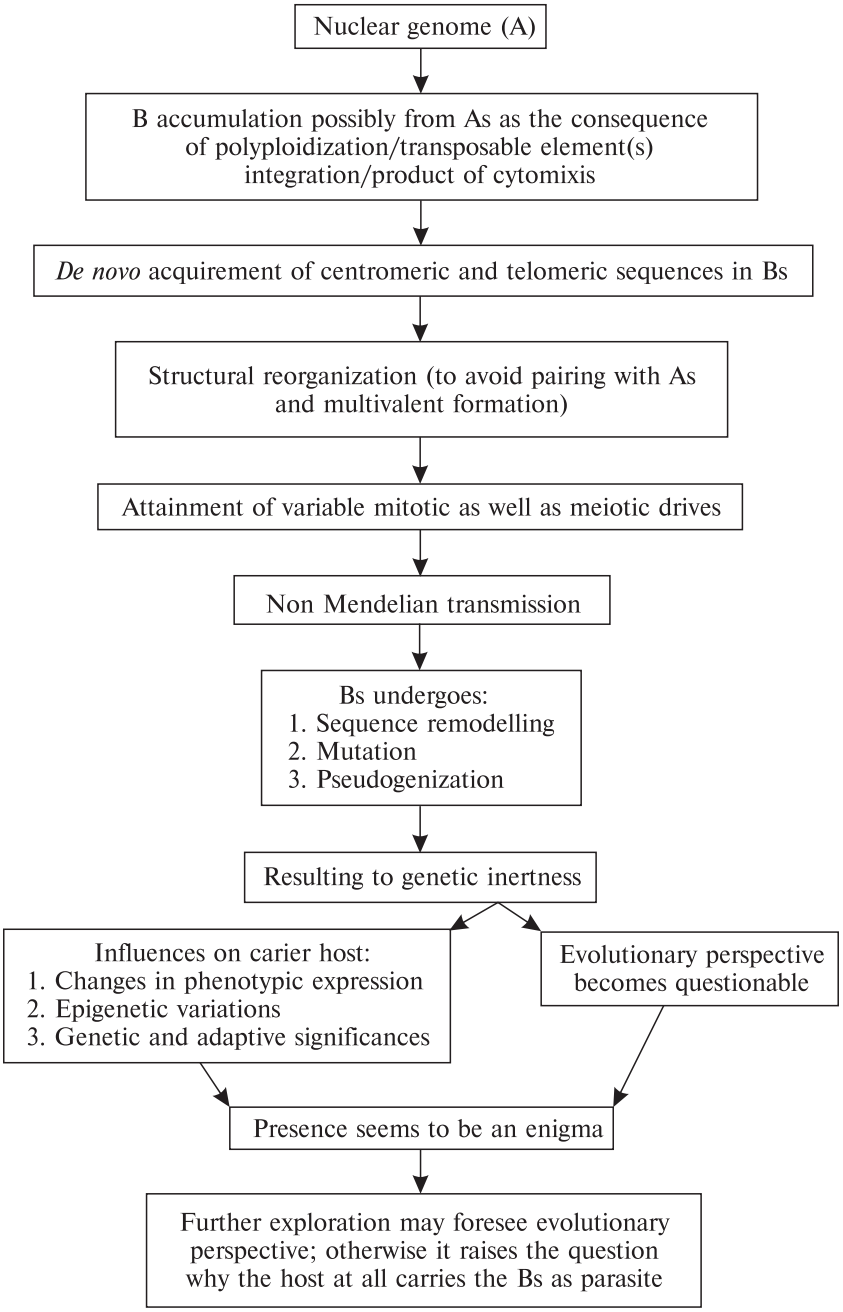
B chromosome origin remains to be a mystery till date. Molecular studies performed involving B systems in angiosperms indicate that Bs possibly do not have a single mode of origin rather they might have arisen through diversified ways. Experimental evidences suggested are significant, but it is rather difficult to elucidate the exact path of B chromosome origin.

Evolutionary aspects. B chromosome origin is concomitantly associated with its evolution. The prime significance of evolution is stabilization of B elements and gaining species level potentiality. Repeat family amplification possibly is the mechanism of nascent chromosome fragment stabilization and positive selection [142]. Rapid B specific sequence amplification along with reduction in selection pressure on genetic integrity possibly provided thrust for structural modification of Bs and establishment of drive mechanism [8]. Structural modification plays a predisposition factor for synaptic failure of B element with their progenitor leading to genomic isolation [14]. The functional autonomy of the nascent Bs are restored by the *de novo* addition of centromeric repeats, and merging of telemetric repeats leads to structural stabilization of B elements [67]. Epigenetic events are reported to play an important role in inducing centromeric activity in B elements [143]. A-derived proto B chromosome possibly encompasses gene(s) in more than one copies sharing homology with As, which must have been down-regulated by dosage compensating mechanism for multicopy gene expression in the course of evolution [8].

Insertion of mobile genetic element in rye possibly mediated structural variability of Bs that of with As [14]. Klemme et al. [144] illustrated a model explaining accumulation as well as depletion of B-located retrotransposons. During barley speciation retroelement 'Sabrina' is reported to be predominant in both neoB and A genome fraction [145]. In course of evolution dispensable nature and lack of selection pressure of B elements result into accumulation of newly evolving retroelement *Revolver*, which possibly differentiated Bs from As [144].

Origin of B supernumerary element coupled with long term evolution indicates isolation of the selfish element from the rest of the genome fraction. After derivation of proto B element from As following consequences possibly have occurred 1) *de novo* incorporation of telomeric and centromeric sequence for immediate protection of nascent B elements from DNA degradation enzyme attack, 2) attaining meiotic transmissional potentiality and 3) amplification of both B specific and non-specific repeat sequences thereby preventing multivalent formation between standard A set and B elements by providing distinctiveness in chromatin condensation pattern.

Epigenetic changes. Epigenetic changes of B elements include 1) hypermethylation-induced transcriptional inactivation of B-specific repeat sequence (Bd49) in *B. dichromosomatica* [146], 2) demethylation influencing mitotic non-disjunction in *Secale cereale* [147], 3) transcriptional regulation following histone acetylation coupled with chromatin packaging leading to gene silencing in *B. dichromosomatica* [79], 4) chromosome condensation facilitating rDNA transcriptional blockage during mitosis in *Allium* spp. [148], and among others. Epigenetic changes



A comprehensive diagrammatic representation of Bs in angiosperms

possibly signify the following 1) prevention of A-neoB homologous pairing, 2) after-birth B element degradation by DNase and 3) genetic isolation from progenitor A genome.

In course of evolution, gene sequence of B element underwent several truncation modifications as sequence remodelling, mutation and pseudogenization resulting in apparent inertness of the supernumerary element.

Significant role of Bs on host species. B chromosomes though reported to be nuclear parasites and supernumerary in nature, several significances are documented.

Phenotypic consequences. Nuclear disposition of B elements shows the wide range (morpho-physiological attributes, A chromosome pairing behaviour, fertility among others) of phenotypic effects, significant as well

as detrimental to host; although, at low number they tend to be neutral [9, 13, 14, 20, 149]. B chromosome accumulation in odd and even numbers in rye is reported to cause differential phenotypic expression [150]. B chromosome effects noted in a species population possibly depends upon the prevailing environmental conditions, and it may be both spatial and temporal [14].

It is rather noteworthy to ascertain whether B chromosome effect is consistent in a given species growing under different eco-physiological conditions, and also in different generation(s). If so, then only its role in evolution may be justified.

Genetic and adaptive influence: 1) post-translational modifications, like H3 phosphorylation [151]; 2) genetic analysis for mapping of genes in maize following A-B translocations [152, 153]; 3) identification of centromere structure and size in maize [123]; 4) potentiality to control normal pairing in some allopolyploid hybrids [154, 155]; 5) influencing recombination through chiasma modulation in rye and distribution in the A chromosomes [20]; 6) adaptational potentiality in *Allium schoenoprasum* [10, 11]; 7) modifying and exploring the A genomes of their host species [67], and among others. The significance of B chromosomes taken together may provide insight to the understanding of structure, origin and evolution.

Insight to the phenomenon. Summarizing B chromosomes on variable aspects, few questions are raised and they are 1) why are Bs then not present in all angiosperms? 2) What are the possible reason(s) behind the distributional biasness of B elements between monocots and eudicots? 3) If larger genome size favours the presence of Bs over their absence, then why there exist no correlation between B number and ploidy level? 4) How is the preferential transmission novelty established in nascent B elements? 5) What is the mechanism behind univalent B localization towards pole during MI? 6) Is there any signalling pathway mediating preferential fertilization of egg with B pollen than 0B? 7) Is any mechanism prevails to explain B chromosome polymorphism within an individual? 8) What are the determining factors maintaining equilibrium between accumulation and harmful effects of B elements? 9) How do the B elements possessing rDNA sequence and NOR gene in angiosperm, cause phenotypic effects? 10) What is the conjugative mechanism behind agglomerization of A genome fraction with that of organellar genome leading to the origin of B elements? 11) What are the possible regulatory mechanisms behind genome remodelling in nascent Bs? 12) What are the possible switching mechanisms for transcriptional activation of B segment regulating meiotic drive during pollen development and anthesis? 13) How does B mediate alteration of chiasma distribution and bivalent pairing in As? and 14) If Bs are mostly non-essential elements, why are they retained in the host as a separate entity?

Conclusion. Considering the aspects discussed in the article it seems that the presence of Bs in angiosperms is still an enigma (Figure). Bs are not reported from all angiosperm members till date. Genome size databases do not usually indicate the existence of B chromosomes [67]. Further, scientific quest may unravel the unexplored information about Bs to foresee their evolutionary perspectives, otherwise hundred years research on B chromosome in angiosperm will remain as a dilemma to scientific community.

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B-ХРОМОСОМЫ У ПОКРЫТОСЕМЕННЫХ

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В обзоре представлены результаты исследований B-хромосом у покрытосеменных. Рассмотрено распространение, морфология, полиморфные формы, гетерогенность фаз деления, организация хроматина и типы генов, результаты секвенирования, происхождение, эволюционные аспекты и значение в клетках хозяина с целью предсказать эволюционные перспективы, которые все еще остаются загадкой. Вне зависимости от происхождения B-хромосом они, очевидно, претерпели ряд модификаций, таких как инсерции центромерных и теломерных последовательностей, структурные реорганизации, ход митоза и мейоза, но вместе с тем проявляют генетическую инертность и присутствуют в клетках хозяина как «эгоистичная» ДНК. В этом отношении поднимается несколько вопросов. В дальнейшем научный поиск может расшифровать неизвестную информацию о B-хромосомах, чтобы определить их эволюционные перспективы, если они существуют.

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