

INTERNATIONAL
REVIEW OF CYTOLOGY

VOLUME 40

INTERNATIONAL Review of Cytology

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VOLUME 40



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B-Chromosome Systems in Flowering Plants and Animal Species

R. N. JONES

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I. Introduction

In eukaryotes each chromosome of the basic complement makes a vital and unique contribution to the genome. Physiologically, a haploid set is the genetic minimum for an organism to function. But for mechanical reasons those species that reproduce sexually require at least a diploid complement in order to accomplish orderly segregation and recombination at meiosis. With few exceptions (e.g., hyacinths), any form of numerical variation other than some exact multiple of the basic complement, as in trisomics or other aneuploids, is not compatible with normal development and reproduction. There is a requirement for the individual chromosomes of the basic complement to be present in a strict numerical relationship to one another. This requirement is not mandatory though for certain nonessential chromosomes which are different from and additional to those of the basic set. Many species of higher plants and animals have what appear to be "optional extras," called *B chromosomes*,

which are outside the laws of classic genetics and a perpetual source of embarrassment to cytologists.

One of the first reports of the occurrence of B chromosomes was given by Stevens (1908), who described the presence of small additional chromosomes appearing in variable numbers in about 50% of random collections of the animal species *Diabrotica soror* and *Diabrotica 12-punctata* (Coleoptera). Stevens adopted the term supernumerary which Wilson (1907) had earlier used to describe certain extra chromosomes in *Metapodius* (Hemiptera). In plants, Kuwada (1915, 1925), Reeves (1925), and Fisk (1925) commented on the variable chromosome number of maize, but it was Longley (1927) who first distinguished these extra chromosomes in maize as supernumerary and presented a major work on their character and behavior. Randolph (1928) classified the extra chromosomes of maize into three types: A—duplicates of members of the typical set; B—chromosomes of approximately the same size as the smallest members of the typical set but differing from them in form and behavior; and C—diminutive chromosomes (derivatives of the B types). Thus the term B chromosome was introduced to describe extra chromosomes which have little if any effect on visible characters of the plant, which are not homologous with the A chromosomes of the normal complement, and which are extremely irregular in their meiotic distribution. B Chromosomes are now known under a variety of different names (see Battaglia, 1964b), including supernumerary and accessory, which are the most common alternatives. This confusion in the nomenclature reflects the struggle that successive generations of cytologists have had to define them unambiguously.

B Chromosomes are dispensable and nonhomologous with A chromosomes. These two characteristics above all others most sharply differentiate them from members of the basic A-chromosome complement. For practical purposes of definition and description, however, they are best considered from a much broader standpoint and with reference to a unique set of attributes:

1. Bs may be present or absent within individuals of a species.
2. When present they vary in number among individuals and among different populations.
3. Their inheritance is non-Mendelian. B Chromosomes are unstable during somatic cell division and/or meiosis. Their maintenance in a population depends on an equilibrium between forces of elimination and accumulation.
4. They are generally smaller than A chromosomes and devoid of major genes.

5. Bs adversely affect vigor and fertility, especially when present in high numbers. The genetic effects are of a polygenic nature, and they are phenotypically undetectable in low numbers.

6. They alter the nuclear phenotype. Changes occur in such fundamental processes as cell cycle time, gene activity, and A-chromosome behavior at meiosis.

These exceptional characteristics are of themselves, interesting enough, but the main reason why B chromosomes are presently attracting so much attention is on account of their widespread distribution and their potential as an experimental system.

II. Distribution

Information relating to numbers of B-chromosome-containing species has been given by Melander (1950), Makino (1951), and White (1973) for animals, by Darlington and Wylie (1955) and Federov (1969) for plants, and by Battaglia (1964b) for plants and animals. For animals the number is small, 116 in the present survey (Table I). They occur mainly in the Coleoptera and Orthoptera. The Orthoptera are especially suitable for cytological studies, and this no doubt is reflected in the extent to which B chromosomes have been found in this group. Their discovery in mammalian species is recent, as indeed is the method of chromosome analysis based on blood culture, and only six species are known to carry them. In plants, B chromosomes occur much more extensively. Darlington and Wylie (1955) list the chromosome numbers of over 17,000 species of flowering plants, of which 139 (0.8%) have Bs. Federov (1969) lists chromosome numbers of more than 35,000 species of flowering plants of which 381 (1.1%) contain Bs. In Battaglia's survey, over 200 species of flowering plants with Bs were listed, together with a few animals and some mosses. The present survey (Tables I and II) records the occurrence of B chromosomes in 591 species from 219 genera of flowering plants, of which 6 are gymnosperms and the rest angiosperms. They are about equally divided between the dicotyledons (297) and the monocotyledons (294). The number is slightly overestimated in so far as polyploid members of some species have been recorded separately. However, we have to remember that many chromosome counts are based on but a single individual of a species, and thus many B chromosomes have probably been overlooked. Add to this the fact that a large number of both plant and animal species have not as yet been examined cytologically at all, and it becomes apparent that the true number of B-chromosome-containing species is probably far in excess of that listed in Table I. In

TABLE I

B CHROMOSOMES IN FLOWERING PLANT AND ANIMAL SPECIES^a

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs ^b	Reference
Gymnosperms				
Cupressaceae				
<i>Cupressus glabra</i>	2X	22	1	Hunziker (1961)
Ephedraceae				
<i>Ephedra foliata</i>	2X	14	+B	Rao (1968)
Pinaceae				
<i>Picea obovata</i>	2X	24	0-3	Krukliis (1971)
<i>Picea sitchensis</i>	2X	24	0-2	Moir and Fox (1972)
Taxaceae				
<i>Taxus canadensis</i>	2X	24	1	Dark (1932)
Taxodiaceae				
<i>Sequoia sempervirens</i>	6X	66	0-1	Saylor <i>et al.</i> (1970)
Angiosperms—Dicotyledons				
Boraginaceae				
<i>Anchusa azurea</i>	4X	32	1-4	Britton (1951)
<i>Onosma albo-roseum</i>	3X	21	1	Teppner (1971)
<i>Onosma albo-roseum</i>	6X	42	1	Teppner (1971)
<i>Onosma javorkae</i>	2X	14	3-4	Teppner (1971)
Campanulaceae				
<i>Campanula cenisia</i>	2X	34	3	Podlech and Damboldt (1963)
<i>Campanula cochleariifolia</i>	2X	34	0-3	Gadella (1964); Gadella and Kliphius (1970)
<i>Campanula ficarioides</i>	6X	102	2-3	Geslot and Medus (1971)
<i>Campanula hispanica</i>	?	72	0-1	Geslot and Medus (1971)
<i>Campanula latifolia</i>	2X	34	3-5	Gadella (1964)
<i>Campanula oblongifolia</i>	?	90	2	Podlech and Damboldt (1963)
<i>Campanula persicifolia</i>	2X	16	4	Böcher (1964)
<i>Campanula rotundifolia</i>	4X	68	0-4	Böcher (1960, 1963); Gadella (1964)
<i>Campanula rotundifolia</i>	6X	102	0, 3, 5	Geslot and Medus (1971)
<i>Campanula serrata</i>	2X	34	2	Podlech and Damboldt (1963)
<i>Phyteuma spicatum</i>	2X	22	1-4	Ochlewska (1965)
Caprifoliaceae				

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Sambucus adnata</i>	2×	38	0-1	Mehra and Bawa (1968)
<i>Sambucus canadensis</i>	2×	38	0-2	Mehra and Bawa (1968)
Chenopodiaceae				
<i>Salicornia herbacea</i>	4×	36	2	Maude (1940)
Compositae				
<i>Achillea asplenifolia</i>	2×	18	+B	Ehrendorfer (1957, 1959, 1961)
<i>Achillea collina</i>	4×	36	+B	Ehrendorfer (1959, 1961)
<i>Achillea crithmifolia</i>	2×	18	+B	Ehrendorfer (1959, 1961)
<i>Achillea millefolium</i>	6×	54	+B	Ehrendorfer (1960, 1961)
<i>Achillea roseo-alba</i>	2×	18	+B	Ehrendorfer (1959, 1961)
<i>Achillea setacea</i>	2×	18	1-6	Ehrendorfer (1960, 1961)
<i>Ageratum paleaceum</i> ^c	2×	22	1	Turner <i>et al.</i> (1962)
<i>Anthemis ruthenica</i>	2×	18	0-3	Mitsuoka and Ehrendorfer (1972)
<i>Aspilia africana</i> ^c	?	68	2	Turner and Lewis (1965)
<i>Aster ageratoides</i>	2×	18	0-6	Matsuda (1970a,b)
<i>Aster ageratoides</i>	4×	36	0-4	Matsuda (1970a,b)
<i>Aster ageratoides</i>	6×	54	0-5	Matsuda (1970a,b)
<i>Aster scaba</i>	2×	18	0-14	Matsuda (1970a,c)
<i>Aster semianplexicaulis</i>	2×	18	1-4	Matsuda (1964)
<i>Astranthium purpurascens</i>	4×	16	1-2	De Jong (1965)
<i>Bahia xylopoda</i>	?	22	1	Powell and Turner (1963)
<i>Bidens taitensis</i>	4× - 2	46	1	Turner and Lewis (1965)
<i>Brachycome curvicaipa</i>	2×	8	4-5	Smith-White <i>et al.</i> (1970)
<i>Brachycome lineariloba</i>	2×	4	0-22	Smith-White (1968); Smith-White and Carter (1970); Smith-White <i>et al.</i> (1970)
<i>Brachycome marginata</i>	2×?	16	0-4	Smith-White <i>et al.</i> (1970)

(Continued)

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Brachycome marginata</i>	3×?	24	0-3	Smith-White <i>et al.</i> (1970)
<i>Brachycome nivalis</i>	2×?	18	1-2	Smith-White <i>et al.</i> (1970)
<i>Brachycome papillosa</i>	2×	8	2	Smith-White <i>et al.</i> (1970)
<i>Carduus crispus</i>	2×	16	1-4	Górecka (1956)
<i>Carduus defloratus</i>	2×	20	0-3	Favarger and Küpfer (1970)
<i>Centaurea arguta</i>	?	30	0-1	Bramwell <i>et al.</i> (1971)
<i>Centaurea behen</i>	?	36	3	Federov (1969)
<i>Centaurea carduiiformis</i>	2×	20	+B	Federov (1969)
<i>Centaurea huettii</i>	?	40	2	Federov (1969)
<i>Centaurea phaeopappoides</i>	?	26	3	Federov (1969)
<i>Centaurea rhenana</i>	2×	18	0-2	Skalínska <i>et al.</i> (1959)
<i>Centaurea scabiosa</i>	2×	20	0-22	Fröst (1948, 1956, 1957, 1958a,b)
<i>Centaurea subciliaris</i>	2×	18	2	Phitos and Damboldt (1971)
<i>Centaurea subciliaris</i>	4×	36	0, 4	Phitos and Damboldt (1971)
<i>Centaurea taochia</i>	?	30	+B	Federov (1969)
<i>Chrysanthemum corymbosum</i>	2×	18	0, 2	Dowrick (1952)
<i>Chrysanthemum heterophyllum</i>	8×	72	0, 3	Favarger (1963)
<i>Chrysanthemum ircutianum</i>	4×	36	0-1	Favarger (1963)
<i>Chrysanthemum millefolium</i>	2×	18	0-1	Dowrick (1952)
<i>Chrysanthemum montanum</i>	6×	54	0-3	Favarger (1963)
<i>Cirsium acaule</i>	2×	34	6	Moore and Frankton (1962)
<i>Cirsium fontinale</i>	2×	34	1	Moore and Frankton (1963)
<i>Cirsium hookerianum</i>	2×	34	2	Moore and Frankton (1965)

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Cirsium scopulorum</i>	2×	34	2	Moore and Frankton (1965)
<i>Crepis capillaris</i>	2×	6	0-4	Abraham <i>et al.</i> (1968); Barthelmes and Bauchinger (1962); Röthlisberger (1970); Rutishauser (1960a, 1963); Rutishauser and Röthlisberger (1966); Schweizer (1973)
<i>Crepis conyzaeifolia</i>	2×	8	0-8	Fröst and Östergren (1959); Fröst (1962, 1964)
<i>Crepis pannonica</i>	2×	8	0-3	Fröst and Östergren (1959); Fröst (1960)
<i>Crepis sancta</i>	?	?	+B	Nazarova (1969)
<i>Crepis sibirica</i>	2×	10	0-2	Swezy (1935)
<i>Crepis syriaca</i>	2×	10	0-8	Cameron (1934); Babcock (1947)
<i>Dimorphothea pluvialis</i>	?	17	+B	Gupta (1969)
<i>Franseria chenopodiifolia</i>	4×	72	2	Payne <i>et al.</i> (1964)
<i>Gnaphalium luteo-album</i>	2×	14	0-1	Larsen (1960a)
<i>Grindelia arenicola</i>	4×	24	1	Raven <i>et al.</i> (1960)
<i>Grindelia rubricaulis</i>	2×	12	1	Raven <i>et al.</i> (1960)
<i>Haplopappus gracilis</i>	2×	4	0-6	Jackson (1960); Jackson and Newmark, (1960); Östergren and Fröst (1962); Pritchard (1968)
<i>Haplopappus spinulosus</i>	2×	8	0-4	Raven <i>et al.</i> (1960); Li and Jackson (1961)
<i>Haplopappus validus</i>	2×	14	0-6	Smith (1968)
<i>Hedypnois rhagadioloides</i>	?	12	1	Larsen (1956)
<i>Inula graveoleus</i>	?	20	0-2	Nilsson and Lassen (1971)

(Continued)

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Kalimeris dentata-incisa</i> ^c	8×	72	2	Shindo (1965)
<i>Kalimeris pseudo-yomena</i> ^c	7×	63	2	Shindo (1965)
<i>Leontodon hispidus</i>	2×	14	1	Bergman (1935)
<i>Leucanthemum croaticum</i>	6×	54	0-2	Papeš (1971)
<i>Leucanthemum croaticum</i>	8×	71, 72	1-2	Papeš (1971)
<i>Leucanthemum leucolepis</i>	4×	36	1	Papeš (1971)
<i>Leucanthemum liburnicum</i>	8×	72	1-2	Papeš (1971)
<i>Leucanthemum montanum</i>	5×	45	1-2	Papeš (1971)
<i>Leucanthemum montanum</i>	8×	70-73	0-2	Papeš (1971)
<i>Leucanthemum species hybrid</i>	7×	63	2-10	Papeš (1971)
<i>Leucanthemum vulgare</i>	4×	36	1-8	Papeš (1971)
<i>Leucanthemum vulgare</i>	6×	54	1-2	Papeš (1971)
<i>Liatris pychnostachya</i>	2×	20	1-3	Gaiser (1949)
<i>Machaeranthera canescens</i>	2×	8	1	Solbrig <i>et al.</i> (1964)
<i>Matricaria maritima</i>	2×	18	0-2	Mulligan (1959)
<i>Melampodium flaccidum</i>	?	50	1	Turner and King (1964)
<i>Olearia argophylla</i>	12×	108	1	Solbrig <i>et al.</i> (1964)
<i>Parthenium argentatum</i>	2×	36	0-5	Bergner (1946); Catcheside (1950)
<i>Parthenium argentatum</i>	3×	54	+B	Bergner (1946); Catcheside (1950)
<i>Parthenium argentatum</i>	4×	72	+B	Bergner (1946); Catcheside (1950)
<i>Perityle hofmeisteria</i> ^c	?	32	1	Turner and Flyr (1966)
<i>Perityle microglossa</i> ^c	?	34, 36	1	Turner and Flyr (1966)
<i>Perityle microglossa</i> ^c	?	92	8	Turner <i>et al.</i> (1962)
<i>Polymnia maculata</i>	?	66	1	Wells (1965)
<i>Pseudocappia arenaria</i> ^c	?	36	1	Powell and Turner (1963)
<i>Rudbeckia serotina</i>	2×	38	1	Mulligan (1959)
<i>Schkuhria pinnata</i> ^c	4×	40	1	Turner <i>et al.</i> (1962)
<i>Senecio adonidifolius</i>	8×	40	2	Palmblad (1965)
<i>Senecio capitatus</i>	?	96	2	Federov (1969)

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Senecio confusus</i> ^c	?	90	5	Turner <i>et al.</i> (1962)
<i>Senecio foetidus</i>	?	40	1	Palmblad (1965)
<i>Senecio fremontii</i>	?	40	1	Federov (1969)
<i>Senecio hieronymi</i>	2×	20	0-4	Afzelius (1959)
<i>Senecio pancicalyailatus</i> ^c	?	42	1	Turner and Lewis (1965)
<i>Senecio petasites</i>	?	60	6	Ornduff <i>et al.</i> (1963)
<i>Silphium trifoliatum</i>	?	14	1-4	Fisher and Cruden (1962)
<i>Solidago arguta</i>	2×	18	0-4, 6	Beaudry (1963)
<i>Solidago altissima</i>	6×	54	0-2, 5	Beaudry (1963); Beaudry and Chabot (1959)
<i>Solidago bicolor</i>	2×	18	0-1	Beaudry (1963)
<i>Solidago canadensis</i>	2×	18	0-3	Beaudry and Chabot (1959)
<i>Solidago curtisii</i>	2×	18	0-6, 10	Beaudry (1963)
<i>Solidago fistulosa</i>	2×	18	0-10	Beaudry (1963)
<i>Solidago gigantea</i>	2×	18	0-4	Beaudry (1963); Beaudry and Chabot (1959)
<i>Solidago gigantea</i>	4×	36	1	Beaudry and Chabot (1959)
<i>Solidago graminifolia</i>	2×	18	2	Beaudry (1963)
<i>Solidago hispida</i>	2×	18	2	Kapoor and Beaudry (1966)
<i>Solidago lepidia</i>	2×	18	0, 1	Beaudry and Chabot (1959)
<i>Solidago leptocephala</i>	6×	54	1	Kapoor and Beaudry (1966)
<i>Solidago macrophylla</i>	2×	18	0-2	Beaudry and Chabot (1959)
<i>Solidago nemoralis</i>	2×	18	0-3	Beaudry and Chabot (1959)
<i>Solidago puberula</i>	2×	18	0-3	Beaudry (1963)
<i>Solidago purshii</i>	2×	18	0-2, 4	Beaudry and Chabot (1959)
<i>Solidago racemosa</i>	6×	54	0-2	Beaudry (1963)
<i>Solidago randii</i>	4×	36	0-1	Beaudry (1963)
<i>Solidago roanensis</i>	2×	18	0-1	Beaudry (1963)
<i>Solidago sempervirens</i>	2×	18	0-1	Beaudry and Chabot (1959)

(Continued)

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Taraxacum alpicola</i>	3×	24	2	Takemoto (1954)
<i>Taraxacum japonicum</i>	2×	16	2	Takemoto (1954)
<i>Taraxacum officinale</i>	3×	24	2	Takemoto (1954)
<i>Taraxacum platycarpum</i>	2×	16	2	Takemoto (1954)
<i>Vernonia karwinskiana</i> ^c	?	34	1	Turner <i>et al.</i> (1962)
<i>Wulfia baccata</i> ^c	?	60	2	Turner and Irwin (1960)
<i>Xanthisma texanum</i>	2×	8	0-4	Berger and Witkus (1954); Berger <i>et al.</i> (1955, 1956); Semple (1972)
<i>Zaluzania montagnifolia</i> ^c	?	34	+B	Powell and Turner (1963)
<i>Zinnia acerosa</i> ^c	?	20, 38	2	Torres (1962)
<i>Zinnia haageana</i> ^c	?	22	2	Powell and Turner (1963)
<i>Zinnia tenella</i>	?	22	1-2	Powell and Turner (1963)
Convolvulaceae				
<i>Ipomoea aquatica</i>	2×	30	1	Krishnappa (1971)
Cornaceae				
<i>Aucuba japonica</i>	4×	32	2	Yamamoto (1937); Viinikka (1970)
<i>Cornus rugosa</i>	2×	22	0-1	Clay and Nath (1971)
Crassulaceae				
<i>Aichryson pachycaulon</i> ^c	4×	60	2	Uhl (1961)
<i>Kalanchoe calycinum</i>	2×	34	4	Warden (1958, 1959)
<i>Kalanchoe gastonis-bonnieri</i>	2×	34	1-4	Uhl (1948); Warden (1959)
<i>Kalanchoe pinnata</i> ^c	2×	40	+B	Warden (1959)
<i>Sempervivum montanum</i> ^c	?	44	+B	Uhl (1961)
Cruciferae				
<i>Arabis alpina</i> ^c	2×	16	1	Titz (1967)
<i>Arabis divarica</i>	?	13, 20	2	Mulligan (1964)
<i>Arabis holboellii</i>	2×	14	+B	Mulligan (1964); Packer (1964)
<i>Arabis holboellii</i>	3×	21	2	Böcher and Larsen (1950); Mulligan (1964)
<i>Arabis procurrens</i>	2×	16	1-2	Burdet (1967)
<i>Arabis procurrens</i>	3×	24	2	Burdet (1967)

TABLE I (Continued)

Flowering plants				
Family, genus, and species	Ploidy	2n	Number of Bs	Reference
<i>Arabis vochinensis</i>	2×	16	1-2	Burdet (1967)
<i>Cochlearia anglica</i>	8×	48	+B	Saunte (1955)
<i>Cochlearia officinalis</i>	4×	24	+B	Saunte (1955)
<i>Cochlearia pyrenaica</i>	2×	12	0-4	J. J. B. Gill (1971a)
<i>Cochlearia scotia</i>	2×	24	0-4	J. J. B. Gill (1971b)
<i>Diplotaxis muralis</i>	2×	18	2	Baez-Major (1934)
<i>Diplotaxis tenuifolia</i>	?	20	2	Baez-Major (1934)
<i>Draba norvegica</i>	6×	48	4	Böcher (1966)
<i>Iberis saxatile</i>	2×	22	2	Manton (1932)
<i>Iberis semperlorens</i>	2×	22	1	Manton (1932)
<i>Lunaria annua</i>	4×	28	2	Manton (1932)
<i>Lunaria rediva</i>	4×	28	2	Manton (1932)
<i>Matthiola incana</i>	2×	14	1-2	Lesly and Frost (1928)
<i>Sisymbrium officinale</i>	2×	14	4	Baez-Major (1934)
Cucurbitaceae				
<i>Melothria maderaspatana</i>	2×	22	1-2	Kumar and Vishveshwaraiah (1951)
Epacridaceae				
<i>Brachyloma preissii</i>	2×	14	0-1	Darlington and Wylie (1955)
<i>Leucopogon oldfieldii</i>	2×	22	0-2	Darlington and Wylie (1955)
<i>Leucopogon revolutus</i>	2×	22	0-3	Darlington and Wylie (1955)
Geraniaceae				
<i>Geranium erianthum</i>	2×	28	1-2	Shimizu (1971)
<i>Geranium tripartitum</i>	2×	28	2	Shimizu (1971)
<i>Geranium wilfordi</i>	2×	28	2	Shimizu (1971)
Labiatae				
<i>Lamium album</i>	2×	18	1	Gill (1970)
<i>Mentha spicata</i>	8×	48	2	Ruttle (1931)
<i>Pycnanthemum flexuosum</i>	?	36	1	Chambers (1961)
<i>Pycnanthemum pilosum</i>	?	78	1	Chambers (1961)
<i>Salvia plebeia</i>	2×	16	1	L. S. Gill (1971a)
<i>Scutellaria repens</i>	2×	20	1	Gill (1970)
Lauraceae				
<i>Beilschmiedia gam-mieana</i>	2×	24	0-2	Mehra and Bawa (1968)
<i>Neolitsea zeylanica</i>	4×	48	0-5	Mehra and Bawa (1968)

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