PHYLETIC HOT SPOTS FOR B CHROMOSOMES IN ANGIOSPERMS

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Abstract.—We determined whether supernumerary B chromosomes were nonrandomly distributed among major angiosperm lineages and among lineages within families, as well as the identity of lineages with unusually high B-chromosome frequencies (hot spots). The incidence of B chromosomes for each taxon was gathered from databases showing species with and without these chromosomes (among species with known chromosome numbers). Heterogeneity was found at all ranks above the species level. About 8% of monocots had B chromosomes versus 3% for eudicots; they were rare in nonmonocot basal angiosperms. Significant heterogeneity in B-chromosome frequency occurred among related orders, families within orders, and major taxa within families. There were many B-chromosome hot spots, including Liliales and Commelinales at the order level. At the family level, there was a trend suggesting that B-chromosome frequencies are positively correlated with genome size.

Key words.—B chromosomes, chromosomal heterogeneity, eudicots, genome size, monocots, phylogeny.

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The chromosomal attributes of flowering plant lineages are far from homogeneous. Some major lineages have unusually high frequencies of a chromosomal feature. For example, the genera of Poaceae are notable for their high incidence of polyploidy (Stebbins 1985). Genera of Onagraceae have an unusually high level of translocations (Levin 2002). Genera of Melanthiaceae have extraordinarily long chromosomes (Leitch et al. 1998). Heterogeneity in karyotypic features is also evident within families. For example festucoid grasses have larger chromosomes than panicoids, which in turn have larger chromosomes than chloridoid grasses (Stebbins 1971).

Students of plant karyotypes have kept track of the number of regular (A) chromosomes, and they have tallied the number of B chromosomes. Jones (1995) estimated that these supernumerary chromosomes occur in about 10–15% of flowering plant species. Their distribution among angiosperm families is quite heterogeneous. They have been described in more than 150 species of Asteraceae and Poaceae and in about 30–50 species in each of several families, including Fabaceae, Liliaceae, Orchidaceae, Campanulaceae, and Ranunculaceae. In most families, however, there have been few or no reports of species with B chromosomes. Overall, more than 1300 species of both eudicots and monocots have these novel elements (Jones 1995).

B chromosomes are often smaller than A chromosomes, do not recombine with any of the As, and vary in copy number among members of the same species (Jones and Rees 1982; Jones 1995). By and large, they lack coding sequences, but nevertheless may have a physiological impact (mostly negative, rarely positive) on their carriers (Bougourd and Jones 1997). Even if they often reduce fitness, they often are maintained by their preferential transmission through the germ line (Jones 1991).

The irregular distribution of B chromosomes among angiosperm families suggests that species in certain families

are more likely to bear them than species in other families. Where are these B-chromosome hot spots? They are not necessarily in the families listed above, because some of them (e.g., Asteraceae and Poaceae) are very speciose and some (e.g., Poaceae and Liliaceae) have been intensively studied karyotypically. Our primary purpose was to document the proportion of B-containing species within families, rather than their numbers, and to assess the level of B-chromosome frequency heterogeneity between families. Another purpose was to determine the extent to which major phylads vary among each other in the frequency of B-carrying species. The third purpose was to assess whether there was significant heterogeneity among genera assigned to different subfamilies or tribes within some large families. We show that there are several hot spots of B-chromosome frequency at different levels of phylogenetic depth.

There are several factors in addition to phylogeny that are associated with the presence or absence of B chromosomes across species, including breeding system (Burt and Trivers 1998), genome size and basic number of A chromosomes (Trivers et al. 2004), and (in mammals) percent acrocentrics among the A chromosomes (Palestis et al 2004a; all studies reviewed in Palestis et al. 2004b). We have previously shown B chromosomes to be positively correlated with genome size among flowering plant species in Britain (Trivers et al. 2004). Although other explanations are possible, it is likely that this correlation results from species with large genomes being better able to tolerate additional genetic material. Here we compare B-chromosome frequency and genome size across families to help explain some of the variation we see in the prevalence of B chromosomes across taxa.

MATERIALS AND METHODS

To ascertain the proportion of species within families, we used the number of B-containing species as described by

Table 1. The prevalence of B chromosomes across major angio-sperm lineages, following Angiosperm Phylogeny Group (2003). Only one statistical comparison is made, because only one pair of sister groups is present. An asterisk indicates significant heterogeneity at the 5% level. The number of species refers to those whose chromosomes have been counted. Totals of subgroups do not add up, because several orders are not included within particular lineages. For example, Myrtales is placed within rosids, but not within either of the two major lineages within rosids, thus the total number of species in eurosids I and eurosids II is less than the number in rosids as a whole.

Taxon	No. species	No. with Bs	Percent with Bs
All angiosperms	23,652	979	4.1
Magnoliids	282	3	1.1
Monocots			
All monocots	5620	447	8.0
Commelinids	2478	189	7.6
Eudicots			
All eudicots	17,717	529	3.0
Core eudicots	16,779	500	3.0
Rosids	5740	145	2.5
Eurosids I	3972	84	2.1
Eurosids II	1191	37	3.1
Asterids	8726	293	3.4
Euasterids I	3914	60	1.5
Euasterids II	4322	214	5.0

Jones (1995) in conjunction with his computer-based dataset (Jones and Díez 2004) on all species with B chromosomes (through 1994), as well as the tabulation of species whose chromosomes numbers have been counted (Index to Plant Chromosome Numbers) provided on the Missouri Botanical Garden web site (http://mobot.mobot.org/W3T/search/ ipcn.html). The number of species with B chromosomes reported here tends to be lower than that reported by Jones (1995), because we do not include unnamed species or additional chromosomal races of one species. Data on average genome size (1C) among families is from Bennett and Leitch (2003). Orders and families were grouped following the classification provided by the Angiosperm Phylogeny Group (2003), with relationships among families within orders largely following Soltis et al. (2000). The major phylads and the orders that they encompass are presented in Tables 1 and 2; families are listed in Table 3.

We sought to determine whether there was B-chromosome frequency heterogeneity among major lineages within families that were large and had many species with B chromosomes. We considered three subfamilies within Asteraceae (Asteroideae, Carduoideae, and Cichorioideae), including 10 tribes within subfamily Asteroideae (Table 4). The tribal affinities for genera of Asteraceae follow the treatment by Panero and Funk (2002). We considered five grass subfamilies (Arundinoideae, Bambusoideae, Chloridoideae, Panicoideae, and Pooideae, Table 4). Species in Pooideae were assigned to either the supertribe Poodae or Triticodae. Species in Panicoideae were assigned either to Andropogodae or Panicodae. We also considered the two monophyletic legume subfamilies (Mimosoideae and Papilionoideae). Within Papilionoideae we contrasted the 10 tribes listed in Table 4. Subfamily and tribal affinities of genera in the grass and legume families

Table 2. The prevalence of B chromosomes across orders. An asterisk indicates significant heterogeneity (at the 5% level or at α levels adjusted for multiple comparisons within a group) within a lineage or among pairs of orders. Statistical comparisons among pairs of orders are performed only for sister groups, and heterogeneity among more than two orders is tested for only if the lineage contains no heterogeneous sister groups.

Taxon	No. species	No. with Bs	Percent with Bs
Magnoliids			
Canellales ¹	2	0	0
Piperales	123	0	0
Laurales	22	3	13.6
Magnoliales	135	0	0 }*
Monocots			
Alismatales	394	20	5.1
Asparagales	2452	184	7.5
Dioscoreales	43	0	0
Liliales	253	54	21.3
Commelinids			
Poales	2235	155	6.9
Commelinales	103	28	27.2
Zingiberales	140	6	4.3 }*
Eudicots			
Ranunculales	905	29	3.2
Proteales	33	0	0
Core eudicots			
Caryophyllales	1592	10	0.6
Santalales	76	13	17.1
Saxifragales	645	39	6.0
Rosids			
Myrtales	577	24	4.2
Eurosids I			1
Celestrales ¹	9	0	0
Malpighiales	676	15	2.2
Oxalidales	49	0	0 ns
Fabales	2040	49	2.4
Rosales Cucurbitales	968 125	15 5	1.5
Fagales	105	0	$\begin{cases} 4.0 \\ 0 \end{cases}$ ns
Eurosids II			~ J J
Brassicales	644	32	4.7
Malvales	266	4	15) 🖟
Sapindales	281	i	0.4 ns $\begin{bmatrix} 1.3 \\ 0.4 \end{bmatrix}$
Asterids			
Ericales	490	19	3.9
Euasterids I			
Gentianales	719	2	0.3
Lamiales	2246	35	1.6 }*
Solanales	949	23	2.4
Euasterids II			2
Apiales	745	7	0.9
Asterales	3321	201	6.1
Dipsacales	256	6	2.3

¹ Taxa with fewer than 10 species are excluded from statistical comparisons.

follow the taxonomic treatments of Kubitzki (1990) as obtained from Mabberley (1997). Legume phylogeny follows Kajita et al. (2001).

Comparisons of the proportion of species with B chro-

mosomes among taxa were performed using the *G*-test for heterogeneity. We compare among sister taxa, because differences among sister taxa are phylogenetically independent (Felsenstein 1985; Burt 1989). Additionally, when a taxon contained no sister groups or none with significant heterogeneity, we also compared across the taxon to determine whether any heterogeneity exists. We are not attempting to trace the evolution of B chromosomes along branches on a tree, but are simply testing whether related groups differ in the prevalence of B chromosomes.

In cases of more than one comparison within a taxon, the G-tests used alpha levels adjusted for multiple comparisons (unplanned tests of the homogeneity of replicates tested for goodness of fit, Sokal and Rohlf 1995). This test is highly conservative, because adjusted alpha levels are very small when several comparisons are made ($\alpha^1 = 1 - [1 - \alpha]^{1/k}$). Only taxa containing at least 10 species with chromosome counts were included, to allow calculation of meaningful percentages and to avoid including poorly studied groups.

One serious problem in any comparison of B chromosomes across taxa is that, by definition, they are not present in all members of a species and thus can be easily overlooked. Therefore, B chromosomes are more likely to be reported in well-studied species and taxa (Palestis et al. 2004b; Trivers et al. 2004). When analyzing the proportion of species with B chromosomes across families as a function of genome size, we added an index of cytogenetic study effort as a variable. It is particularly important to control for study effort here, because angiosperms with large genomes tend to be studied more frequently than those with small genomes (Trivers et al. 2004). This index was calculated as the proportion of species in a family with chromosome counts, multiplied by the proportion of those species with chromosome counts that also have genome size data. The index of study intensity, although rough, is correlated with the proportion of species with B chromosomes across families ($F_{1,50} = 12.06$, P =0.0011, $r^2 = 0.19$; Fig. 1) and thus can be used to statistically control for variation in study effort across families. If the proportion of species with chromosome counts and the proportion with genome size data are used as independent variables, rather than using their product, the results barely change. Additionally, only families containing at least five species with recorded C-values were included, both to avoid including the most poorly studied groups and to allow calculation of mean genome size for a family.

Along with genome size and study effort, the order affiliation of each family was also included in an analysis of covariance, to control for similarity due to phylogeny. The dependent variable was the proportion of species in a family with B chromosomes. This analysis follows the methodology of Barrow and Meister (2003).

RESULTS

Our study included a total of 23,652 angiosperm species, or about 9% of the estimated 260,000 species (Takhtajan 1997). A total of 979 species had B chromosomes (4.1%). There was quite a disparity between monocots and eudicots in B-chromosome representation; 8.0% of the former had them versus only 3.0% of the latter (Table 1).

Table 3. The prevalence of B chromosomes across families. An asterisk indicates significant heterogeneity (at the 5% level or at α levels adjusted for multiple comparisons within a group) within an order or among pairs of families. Statistical comparisons among pairs of families are performed only for sister groups, and heterogeneity among more than two families is tested for only if the lineage contains no heterogeneous sister groups.

lineage contains no heterogeneous sister groups.							
Taxon	No. species	No. with Bs	Percent with Bs				
Nymphaeaceae	33	0	0				
Magnoliids							
Canellales							
Winteraceae ¹	2	0	0				
Piperales							
Piperaceae Aristolociaceae	64 59	0	0				
Magnoliales							
Annonaceae Magnoliaceae	69 66	0	0				
Laurales							
Lauraceae	22	3	13.6				
Monocots							
Alismatales							
Alismataceae	25	0	$\begin{bmatrix} 0 \\ \epsilon \end{bmatrix}$				
Araceae	297	20	6.7	ns			
Hydrocharitaceae	25	0	0	115			
Potamogetonaceae	47	0	0				
Asparagales							
Agavaceae	90	0	0				
Hyacinthaceae	227	33	14.5				
Asparagaceae Alliaceae	181 406	9 43	5.0 \ 10.6 \	*			
Amaryllidaceae	276	32	11.6				
Asphodeliaceae	65	0	0				
Hemerocallidaceae	16	0	0				
Iridaceae Orchidaceae	452 739	17 50	3.8 6.8				
Dioscoreales	137	50	0.0				
Dioscoriaceae	43	0	0				
Liliales	43	O	O				
Liliaceae	172	31	18.0	1			
Colchicaceae	26	0	0	*			
Melanthiaceae	55	23	41.8	J			
Commelinids Poales							
Cyperaceae	382	2	0.5	ns]			
Juncaceae	79	1	1.3	*			
Poaceae	1774	152	8.6	J			
Commelinales							
Commelinaceae	103	28	27.2				
Zingiberales				2			
Marantaceae	11	0	0	l no			
Zingiberaceae Musaceae ¹	122 7	3	2.5 42.9	ns			
Eudicots	,	3	74.7	J			
Ranunculales							
Berberidaceae	62	0	0	ns			
Ranunculaceae	676	27	4.0	ns ns			
Papaveraceae	167	2	1.2	J			
Proteales							
Proteaceae	30	0	0				
Platanaceae ¹	3	0	0				

Table 3. Continued.

Table 3. Continued.

TABL	E 3. Cont	inued.			TABLE 3. Continued.				
Taxon	No. species	No. with Bs	Percent with Bs		Taxon	No. species	No. with Bs	Percent with Bs	
Core eudicots					Sapindales				
Caryophyllales					Meliaceae ¹	8	0	0]
Aizoaceae	96	0	0		Rutaceae	172	ĭ	0.6	ns
Phytolaccaceae ¹	8	0	0		Sapindaceae	60	0	0	(11)
Nyctaginaceae	11	0	0		Anacardiaceae	41	0	0	J
Cactaceae	205	0	0		Asterids				
Amaranthaceae	247	3	1.2	*	Ericales				
Caryophyllaceae	568	0	0_	-	Primulaceae	166	7	4.2	1
Plumbaginaceae	151	1	0.7	\ns	Myrsinaceae	100	0	0	
Polygonaceae	190	3	1.6	J	Polemoniaceae	66	12	18.2	
Droseraceae	38	U	0		Ericaceae	120	0	0	}*
Santalales					Sapotaceae	18	Ő	Ö	
Loranthaceae	69	13	18.8		Theaceae	110	0	0	J
Santalaceae ¹	7	0	0		Euasterids I				_
Saxifragales						250	0	2.5	
Crassulaceae	357	28	7.8	1	Boraginaceae	358	9	2.5	
Hamamelidaceae	32	0	0	ns	Gentianales				
Saxifragaceae	256	11	4.3	110	Rubiaceae	495	0	0]
=	230	11	7.5	J	Apocynaceae	117	0	0	}*
Rosids					Gentianaceae	107	2	1.9	J
Myrtales					Lamiales				
Myrtaceae	139	1	0.7		Gesneriaceae	<i>E E</i>	0	0	1
Melastomataceae	104	0	0	1		55 814	0 14	1.7	
Onagraceae	223	22	9.9	*	Scrophulariaceae	266	2	0.8	
Lythraceae	101	0	0	J	Acanthaceae Lamiaceae	855	1	0.8	
Combretaceae ¹	9	1	11.1		Lannaceae Lentibulariaceae	18	0	0.1	}*
Eurosids I					Orobanchaceae	13	0	0	1
Celastrales					Plantaginaceae	71	11	15.5	
Celastraceae ¹	9	0	0		Verbenaceae	57	7	12.3	
					Oleaceae	97	Ó	0	j
Malpighiales	0.4	0	0	1	Calamalas				
Salicaceae	84	0	0	İ	Solanales		_		ı
Passifloraceae	43	0	0		Convolvulaceae	113	3	2.7	\ns
Violaceae	174	7	4.0	\ns	Solanaceae	478	11	2.3	J
Rhizophoraceae	23 96	0 1	0 1.0		Euasterids II				
Malpighiaceae	256	7	2.7		Apiales				
Euphorbiaceae	230	/	2.1	J	Apiaceae	745	7	0.9	
Oxalidales					Asterales				
Oxalidaceae	49	0	0			2070	170	5 .	
Fabales					Asteraceae	3078	172	5.6	
Fabaceae	2026	49	2.4		Campanulaceae	243	29	11.9	
Polygalaceae	14	0	0		Dipsacales				
	14	U	U		Caprifoliaceae	127	2	1.6	$_{\rm ns}$
Rosales				3	Dipsacaceae	129	4	3.1	J ns
Moraceae	56	0	0		¹ Taxa with fewer than 10 s	pacias ara av	aludad from	ctatictical	compori
Urticaceae	55	2	3.6		sons.	pecies are ex	ciuded iioii	i statisticai	compan-
Ulmaceae	48	1	2.1	}*	sons.				
Rhamnaceae	39	3	7.7						
Rosaceae	770	9	1.2	J					
Cucurbitales					The number of specie	s with chr	omosome	counts, 1	number
Cucurbitaceae	125	5	4.0		with B chromosomes, a				
	123	3	4.0		somes are presented in T				
Fagales				1					
Juglandaceae	15	O	0		the orders that are inclu				
Myricaceae ¹	4	0	0		melinales are the ordina				
Betulaceae	33	0	0	\ns	The tables also indicate	where sig	gnificant	heteroger	neity is
Casuarinaceae ¹	7	0	0		present. Among monoc				
Fagaceae	46	0	0	J	within commelinids. Th				
Eurosids II									
Brassicales					linales with B chromoson				
Brassicaceae	644	32	4.7		in its sister order, Zingi				
	577	32	7.7		much variability in B-ch	nromosome	frequenc	ey among	mono-
Malvales					cot orders. For example,				
Cistaceae	65	0	0		mosome versus 21.3% i				
Malvalaceae	201	4	2.0				2010	spc	-100 111
					Dioscoreales.				

Table 4. The prevalence of B chromosomes across subfamilies, supertribes, and tribes. An asterisk indicates significant heterogeneity at the 5% level or at α levels adjusted for multiple comparisons within a group. Statistical comparisons among pairs of taxa are performed only for sister groups, and heterogeneity among more than two taxa is tested for only if the lineage contains no heterogeneous sister groups.

Taxon	No. species	No. with Bs	Percent with Bs
Poaceae			
Poaceae subfamilies			1
Arundinoideae	132	2	1.5
Bambusoideae Chloridoideae	105 165	0 8	0
Panicoideae	465	44	9.5
Pooideae	907	98	10.8
Panicoidae supertribes			
Andropogodae	156	23	$14.7 \}_*$
Panicodae	309	21	6.8]
Pooidae supertribes			1
Poodae	585	86	14.7 *
Triticodae	322	12	3.7 J
Asteraceae subfamilies			
Asteroideae	2241	145	6.5
Chicorioideae	522	10	1.9 }*
Carduoideae	315	17	5.4
Asteroideae tribes			
Eupatorieae	244	12	4.9
Madieae Millereae	54 43	2 3	3.7 7.0
Heliantheae	304	13	4.3
Coreopsideae	120	0	0
Tageteae	56	0	0 \ *
Anthemideae	326	36	$\frac{11.0}{0.1}$ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \ \
Astereae Gnaphalieae	660 160	60 10	9.1 J 6.3
Senecioneae	274	9	3.3
Fabaceae ¹			J
Fabaceae subfamilies			
Mimosoideae	92	0	0
Papilionoideae	1832	46	2.5
Papilionoideae tribes			
Desmodieae	109	0	0
Amorpheae	17	0	0
Genisteae Crotalarieae	70 131	0 13	0 9.9 }*
Loteae	91	13	1.1
Trifolieae	185	10	5.4 \}*
Vicieae	188	1	0.5
Hedysareae Carmichaelieae	30 15	1 0	3.3
Indigofereae	57	0	0

 $^{^{\}rm I}$ Only apparently monophyletic groups are shown, following Kajita et al. (2001).

The major eudicot lineages generally had lower values than the major monocot lineages. Only one eudicot order (Santalales) has a very high frequency of species with B chromosomes (17.1%), but this proportion is based on a relatively small number of species (n = 76). Most major lineages of eudicots contained fewer than 3.5% B-carrying species (Table 1). Only one pair of major lineages represent true sister

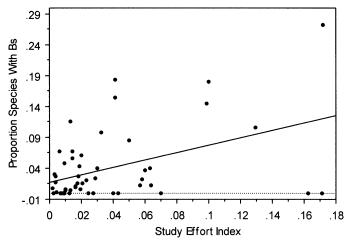


Fig. 1. Correlation between the proportion of species with B chromosomes across families and an index of cytogenetic study effort ($F_{1,50} = 12.06$, P = 0.0011, $r^2 = 0.19$).

groups: euasterids I and II (Angiosperm Phylogeny Group 2003). About 1.5% of euasterids I (Solanales, Gentianales, Lamiales) species had B chromosomes. This value contrasts with 5.0% in the euasterid II lineage (Apiales, Dipsacales, and Asterales), which is a significantly greater percentage (Table 1). However, this difference probably reflects variation at the level of orders and families (see below).

The level of heterogeneity among closely related orders is apparently less in the eudicots than in the monocots, as the range in B-chromosome frequencies is smaller, but significant heterogeneity does exist (Table 2). There is no significant heterogeneity among orders of eurosids I, but there is significant heterogeneity within eurosids II, as B-chromosome frequencies within orders ranged from 0.4% to 4.7%. Significant heterogeneity also exists within both euasterids I and II, with B frequencies among orders ranging from 0.3% to 2.4% in euasterids I and 0.9% to 6.1% in euasterids II.

B chromosomes were generally rare among the nonmonocot basal angiosperms. No B chromosomes have been reported in Nymphaeaceae, but this result is based on only 33 species. Within the magnoliid clade (Magnoliales, Laurales, Canellales, and Piperales), only Lauraceae contain species with reports of B chromosomes (Tables 2, 3).

As the orders were heterogeneous in their B-chromosome frequencies, so were families within 9 of the 19 orders with sufficient data (Table 3). Heterogeneity among families is well exemplified in the monocot order Asparagales. Three families (Alliaceae, Amaryllidaceae, and Hyacinthaceae) all contain between 10% and 15% B-carriers, while the sister family to Alliaceae, Asparagaceae, has significantly fewer (5%), and three other families have none (Table 3). B-chromosome frequencies vary widely in Liliales, ranging from 41.8% of species in Melanthiaceae to 18% in Liliaceae to zero of 26 in Colchicaceae. Within Poales, B-chromosome frequencies range from 0.5% in Cyperaceae to 8.6% in Poaceae. Among eudicots, Myrtales provides another example of heterogeneity, as Onagraceae contains approximately 10% B-carriers, while its sister family, Lythraceae, contain none.

Significant heterogeneity also exists among families within several other eudicot orders (Table 3).

Heterogeneity among subfamilies and among supertribes is well illustrated in Poaceae. B chromosomes are very infrequent in Arundinoideae and Bambusoideae, but appear in approximately 10% of the species in Pooideae and Panicoideae (Table 4). There also are significant differences between the two Pooidae supertribes and between the two Panicoideae supertribes. About 4% of the species of Triticodae have B chromosomes versus 15% for Poodae. Approximately 7% of species in Panicodae have them, compared to 15% in Andropogodae.

Significant heterogeneity also occurs among subfamilies of Asteraceae and among tribes in subfamily Asteroideae (Table 4). Members of the one pair of sister tribes, Anthemideae and Astereae, have similar B-chromosome frequencies, about 9–11% of species. However, across the entire subfamily, B frequency is quite variable.

Turning to Fabaceae, we see that, within Papilionoideae, two sets of sister tribes have strikingly different B-chromosome frequencies (Table 4). Ten percent of species in Crotalarieae have B chromosomes, compared to none in Genisteae. In addition, 5.4% of species in Trifolieae have B chromosomes, compared to 0.5% in Vicieae.

Significant heterogeneity in B-chromosome frequencies is found among genera within some tribes of Asteraceae as well: Anthemideae ($G_8=33.168,\,P<0.0001$), Astereae ($G_{11}=77.721,\,P<0.0001$), and Heliantheae ($G_{11}=36.207,\,P=0.0002$). Comparisons among genera within three other Asteraceae tribes are not significant: Cardueae ($G_9=12.202,\,P=0.202$), Gnaphalieae ($G_5=9.149,\,P=0.103$), and Lactuceae ($G_{10}=17.096,\,P=0.072$). The only other group with sufficient data to compare among genera, supertribe Poodae (Poaceae), shows highly significant variation ($G_{12}=82.027,\,P<0.0001$).

We had hoped to analyze B-chromosome heterogeneity within genera. Unfortunately, phylogenies for B-rich genera were few; and where such existed, species with B chromosomes rarely were included. We would not be surprised to find that B chromosomes were not uniformly distributed among major lineages within genera.

Finally, we compared B-chromosome frequency as a function of 1-C genome size across families. The proportion of species with B chromosomes in a family is correlated with genome size among all families ($F_{1,50}=27.29,\,P<0.0001,\,r^2=0.35;\,\mathrm{Fig.}\,2$), within monocots ($F_{1,14}=6.34,\,P=0.025,\,r^2=0.31$), and within eudicots ($F_{1,32}=8.72,\,P=0.0059,\,r^2=0.21$). After correction for study effort and order affiliation, the relationship between genome size and B-chromosome frequency is nearly significant (analysis of covariance, $F_{1,56}=3.78,\,P=0.057$). Order affiliation has a significant effect on B frequency among families ($F_{32,56}=2.19,\,P=0.0051$). As in Trivers et al. (2004), study effort drops out as a significant variable ($F_{1,56}=1.19,\,P=0.28$) when genome size is included.

DISCUSSION

Our investigations show that there is conspicuous heterogeneity in the frequency of B chromosomes at the tribal level

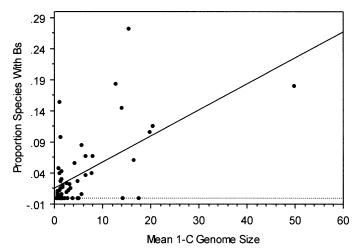


Fig. 2. Correlation between the proportion of species with B chromosomes and mean 1-C genome size among families ($F_{1,50} = 27.29$, P < 0.0001, $r^2 = 0.35$). The strength of the correlation is similar when the one family with an extremely large average genome size (Liliaceae) is excluded ($F_{1,49} = 20.96$, P < 0.0001, $r^2 = 0.30$).

and above in flowering plants. We believe that this pattern will pass the test of time as more species are analyzed and as the number of plants scored per species increases. Because the reporting of B chromosomes is a function of study effort, the values reported here are apt to be lower than actual values. While it is possible that some of the heterogeneity we find among taxa is due to differences in study effort, it is unlikely that study effort alone could explain many of the enormous differences in B-chromosome frequency that we report. There are, for example, some relatively well-studied groups with no or few reports of B chromosomes (e.g., Caryophyllaceae, Lamiaceae; see also Fig. 1).

The two families with by far the largest number of species with B chromosomes are Poaceae and Asteraceae. However, because these families are also highly speciose, several other families actually have a higher proportion of species with B chromosomes. Among orders, the two B hot spots are Liliales and Commelinales. On a percentage basis, B chromosomes are more than twice as common in monocots as in eudicots. B chromosomes are generally rare in the nonmonocot basal angiosperms.

Despite the broad trends summarized above, and a significant effect of order affiliation on B-chromosome prevalence among families, there does not appear to be a strong phylogenetic signal to the distribution of B chromosomes. Although occasionally sister taxa had very similar frequencies of B chromosomes, pairwise comparisions at different levels show that even sister taxa may differ notably in the proportion of species carrying these chromosomal novelties. Similarly, we found highly significant variability among genera in four of seven tribes. Conversely, remotely related taxa may have similar values. These findings are consistent with what is known about the taxonomic disposition of other karyotypic features such as chromosome number, symmetry, and size and the incidence of polyploidy (Stebbins 1971; Levin 2002).

Although the origins of B chromosomes is unknown, they seem to have arisen independently in different lineages based on the phylogenetic distance among groups with high frequencies. The same may also be so within genera and even at the species level. Indeed, one wonders how often B chromosomes are transmitted from a species to its immediate descendants. Because B chromosomes may not be uniformly distributed throughout a species range, carriers of such may not be included in the populations that ultimately diverge to the level of species. This would be especially true if peripheral populations were more likely to give rise to new species, because B chromosomes are less prevalent in them (Jones and Rees 1982). Perhaps some tendency for their genesis is the only common thread that exists between parental species and their derivatives. But we cannot exclude the opposite possibility, that extinction patterns determine entirely B frequency across taxonomic groups.

Given the recurrent origin of B chromosomes throughout flowering plants, we would like to know whether there is something inherent in the genomes of taxa that make their appearance more or less likely. We find a trend suggesting that B chromosomes have a higher frequency in families with relatively large genome sizes. This result is consistent with an earlier study that demonstrated a positive correlation at the species level between genome size and B-chromosome presence in flowering plants in Britain (Trivers et al. 2004; see also Palestis et al. 2004b). Species with very small genomes completely lacked B chromosomes. Perhaps the presence of larger amounts of noncoding DNA allows species to better tolerate the addition of more noncoding DNA, which is what largely constitutes B chromosomes (Puertas 2002; Jones and Houben 2003). Another explanation for the relationship between genome size and B frequency is that the greater amount of noncoding DNA itself is a trigger for Bchromosome production.

The effect of genome size is a product of large A chromosomes, rather than of many A chromosomes, because genome size and chromosome number are inversely correlated (Vinogradov 2001; Trivers et al. 2004). In fact, Trivers et al. (2004) found a significant negative correlation between A chromosome number and B chromosome presence that was independent of genome size. Why this should be true is unclear. Because species with small genomes have small chromosomes and their chromosome number can be high, we cannot rule out one possible artifact: it is probably more difficult to detect B chromosomes in species with many small chromosomes than in species with few large chromosomes. Therefore, the effect of study effort may be underestimated here.

The presence or absence of B chromosomes across species is affected by factors other than genome size. These include breeding system (Burt and Trivers 1998), basic number of A chromosomes (Trivers et al. 2004), and (in mammals) percent acrocentrics among the A chromosomes (Palestis et al 2004a; all studies reviewed in Palestis et al. 2004b).

It is noteworthy that the proportion of species with B chromosomes is similar to or perhaps somewhat less in polyploids than in diploids (Trivers et al. 2004). This is relevant for the genome size discussion, because there is a tendency for polyploids to have less DNA per chromosome set than what one might expect based on the values of their diploid relatives (Levin 2002; Leitch and Bennett 2004; Soltis et al. 2004).

We have shown that angiosperm taxa vary greatly in the

prevalence on B chromosomes and suggest that variation in genome size may explain some of this heterogeneity. Other factors may also contribute to differences in B-chromosome frequency, including breeding system, rates of hybridization, and A-chromosome number. We have found some evidence (D. A. Levin, B. G. Palestis, R. N. Jones, and R. Trivers, unpubl. data) suggesting that taxa with low rates of speciation (Magallon and Sanderson 2001) may be less likely to have reports of B chromosomes. Interestingly, these tend to be ancient taxa, which also have small genome sizes (Leitch et al. 1998; Soltis et al. 2003; Leitch and Bennett 2004). However, these taxa also contain few species and are generally poorly studied.

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