



B chromosomes are more frequent in mammals with acrocentric karyotypes: support for the theory of centromeric drive

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The chromosomes of mammals tend to be either mostly acrocentric (having one long arm) or mostly bi-armed, with few species having intermediate karyotypes. The theory of centromeric drive suggests that this observation reflects a bias during female meiosis, favouring either more centromeres or fewer, and that the direction of this bias changes frequently over evolutionary time. B chromosomes are selfish genetic elements found in some individuals within some species. B chromosomes are often harmful, but persist because they drive (i.e. they are transmitted more frequently than expected). We predicted that species with mainly acrocentric chromosomes would be more likely to harbour B chromosomes than those with mainly bi-armed chromosomes, because female meiosis would favour more centromeres over fewer in species with onearmed chromosomes. Our results show that B chromosomes are indeed more common in species with acrocentric chromosomes, across all mammals, among rodents, among non-rodents and in a test of independent taxonomic contrasts. These results provide independent evidence supporting the theory of centromeric drive and also help to explain the distribution of selfish DNA across species. In addition, we demonstrate an association between the shape of the B chromosomes and the shape of the typical ('A') chromosomes.

Keywords: B chromosomes; centromeric drive; karyotype; meiotic drive; selfish DNA

1. INTRODUCTION

In mammals as a whole, the frequency of acrocentric chromosomes (those with only one long arm) almost exactly equals the frequency of bi-armed ones, but in most species one type greatly predominates (Pardo-Manuel de Villena & Sapienza 2001a). It has been suggested that this distribution reflects an underlying bias during female

meiosis regarding the number of centromeres. When the egg side of the spindle is more efficient at capturing centromeres than the polar body side, more centromeres are favoured over fewer and the karyotype becomes predominately acrocentric (Pardo-Manuel de Villena & Sapienza 2001a). The reverse occurs when the polar body side is more efficient. For example, in humans a single metacentric or sub-metacentric chromosome arisen by the Robertsonian fusion of two acrocentrics is transmitted to more than 50% of the progeny of females when lined up against the two acrocentrics (Pardo-Manuel de Villena & Sapienza 2001b), and humans have mostly metacentric and sub-metacentric chromosomes. In mice, it is the other way around (Pardo-Manuel de Villena & Sapienza 2001a). In addition, in mice, XO females are fertile and the lone X drives (LeMaire-Adkins & Hunt 2000). These facts are consistent with a larger view that rapid evolution of centromeric DNA and the attached histones reflects selection for centromeric drive in female meiosis (Henikoff et al. 2001; Henikoff & Malik 2002).

B chromosomes, a class of selfish genetic elements, provide an opportunity to test this theory. B chromosomes are supernumerary chromosomes found in some but not all individuals within a species, where the A chromosomes are the usual set of chromosomes. B chromosomes typically have a negative phenotypic effect and are often maintained by drive (Jones & Rees 1982; Jones 1991; Camacho 2003). In many species, B chromosomes drive as univalents, where the B provides an extra centromere lined up against no centromere during meiotic segregation. Hence a meiotic bias towards more centromeres should favour B chromosomes, and vice versa. Thus, we expect that B chromosomes will be more frequent in species with relatively more acrocentric chromosomes (or, more precisely, more of their chromosome arms on acrocentrics, because one metacentric has the same number of arms as two acrocentrics and could be formed by the same number of evolutionary events).

2. METHODS

For typical shape of the A chromosomes, we used the data in Pardo-Manuel de Villena & Sapienza (2001a). (These authors defined any chromosomes originally referred to as 'acrocentric' or 'telocentric' as acrocentric, as both are functionally one-armed.) For the presence of B chromosomes we used a database maintained by R.N.J. covering work through 1994, which we updated through 2002 via computer searches (Biological Abstracts, Medline and Web-of-Science). Karyotypes of species with B chromosomes not included in Pardo-Manuel de Villena & Sapienza (2001a) were located using computer searches and an online database of mammalian karyotypes (Institute of Cytology and Genetics 2000). Our dataset contains 1173 species, 57 of which have B chromosomes (45 out of these 57 are rodents). In 51 out of the 53 species for which we have data, the B has been observed as a univalent, although a range of B numbers typically occurs.

We test whether the probability of species harbouring B chromosomes increases as the proportion of autosome arms on acrocentrics increases, using logistic regression. For independent taxonomic contrasts, we treated the A chromosome shape as a discrete variable (more than half versus less than half of arms on acrocentrics), analysed with the methodology described in Burt & Trivers (1998). The taxonomy followed McKenna & Bell (1997).

3. RESULTS AND DISCUSSION

The results are summarized in table 1. Across all mammals, species with B chromosomes average ca. 59% of their autosome arms on acrocentrics, compared with only 36% for species lacking B chromosomes (p < 0.0001, r^2 = 0.048). This comparison is also highly

Table 1. Presence of B chromosomes and shape of the A chromosomes.

(For each group of organisms we show the mean \pm s.e. proportion of autosomes that are acrocentric, and the mean proportion of arms on acrocentrics, among species with and without B chromosomes (Bs). Analysis was performed by logistic regression on the proportion of autosome arms on acrocentric chromosomes versus the presence or absence of B chromosomes.)

	n	proportion of acrocentric autosomes	proportion of arms on acrocentrics
(a) all mammals			
Bs present	57	0.675 ± 0.044	0.592 ± 0.046
Bs absent	1116		
$p < 0.0001, r^2 = 0.048$			
(b) most mammals ^a	0		
Bs present	57	0.675 ± 0.044	0.592 ± 0.046
Bs absent	1015		
		0.439 ± 0.012	0.309 ± 0.011
$p < 0.0001, r^2 = 0.043$			
(c) rodents			
Bs present	45	0.684 ± 0.049	0.602 ± 0.051
Bs absent	346	0.502 ± 0.021	0.432 ± 0.020
$p = 0.0045, r^2 = 0.029$)		
(d) non-rodents ^a			
Bs present	12	0.639 ± 0.103	0.553 ± 0.104
Bs absent	669	0.407 ± 0.014	0.336 ± 0.014
$p = 0.044, r^2 = 0.034$	307	= 0.011	

^a Excludes orders lacking B chromosomes.

significant when orders lacking B chromosomes are excluded and when restricted to rodents, and is significant in non-rodents despite a small number of such species with B chromosomes. In addition, taxonomic contrasts across 25 independent mammalian taxa show a significant association between the frequency of acrocentric A chromosomes and the presence of B chromosomes (p = 0.027; see electronic Appendix A available on The Royal Society's Publications Web site). These results provide strong independent support for the theory of centromeric drive, at least in mammals. Across all levels of analysis, B chromosomes (which increase centromere number) are associated with a higher centromere number in the A chromosomes.

There are, however, species with mostly bi-armed A chromosomes that do have B chromosomes, and four species with B chromosomes have only bi-armed A chromosomes. These exceptions can, in part, be explained if drive in these species occurs at a stage other than female meiosis. They may also reflect inertia, in which after a polarity change favouring B chromosomes, most A chromosomes might still remain bi-armed for some time. In addition, Robertsonian translocations forming bi-armed chromosomes from acrocentrics may create centromeric fragments that occasionally become B chromosomes. It is also possible that B chromosomes that flourish when extra centromeres are being favoured evolve tricks that work even when extra centromeres are being disfavoured.

Our dataset also provides information on the shape of the B chromosomes for 28 species, so we tested for an association between A shape and B shape among species having only acrocentric or only metacentric B chromosomes. Species with acrocentric B chromosomes averaged $75.1 \pm 7.0\%$ (1 s.e., n = 9) of arms on acrocentric A chromosomes, compared with $37.4 \pm 9.8\%$ (n = 10) for species with metacentric B chromosomes (logistic regression, p = 0.0046, $r^2 = 0.306$). This is consistent with the view that B chromosomes are recently derived from A chromosomes or centromeric A fragments. Evidence from grasshopper karyotypes suggests the same association (Camacho 2003). However, it is not uncommon for B chromosomes in one species to have several shapes and sizes, suggesting that changes in B morphology can evolve quickly (López-León et al. 1993). Recent derivation is congenial to the centromeric drive interpretation of our main results, because the dominant shape of A chromosomes is assumed to change frequently over evolutionary time, which can lead to radically different karyotypes among closely related species or populations within a species (Pardo-Manuel de Villena & Sapienza 2001a).

There are, of course, alternative hypotheses. It is possible that single-armed A chromosomes are more likely to donate B chromosomes than are bi-armed A chromosomes, either per chromosome or per arm, but there is no a priori reason to expect such a difference. In addition, any other selection pressure favouring more centromeres over fewer will produce the same association that we have uncovered. We are also aware of the dearth of evidence regarding the way in which B chromosomes usually drive in mammals. In the mammal with the best data (Rattus fuscipes), B chromosomes drive strongly during meiosis in females and show weak or no drive in males (Thomson 1984), as expected if centromeric drive controls the transmission of B chromosomes. The same appears to be true of R. rattus (Camacho 2003), and in both species drive is most pronounced when the B is a univalent. In two other species, drive may instead occur by mitotic instability in males (Patton 1977; Volobujev 1980). However, in these cases nothing is known about drive in females, nor are there any transmission data demonstrating drive in males.

Our results suggest that changes in the direction of centromeric drive favouring acrocentric A chromosomes also increase the success of B chromosomes. Because B chromosomes are often harmful, the presence of B chromosomes may, in turn, select for a change in the direction of centromeric drive favouring bi-armed A chromosomes.

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