

# High-density comparative BAC mapping in the black muntjac (*Muntiacus crinifrons*): Molecular cytogenetic dissection of the origin of MCR 1p+4 in the X1X2Y1Y2Y3 sex chromosome system

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## Abstract

The black muntjac (*Muntiacus crinifrons*,  $2n = 8♀/9♂$ ) is a critically endangered mammalian species that is confined to a narrow region of southeastern China. Male black muntjacs have an astonishing X1X2Y1Y2Y3 sex chromosome system, unparalleled in eutherian mammals, involving approximately half of the entire genome. A high-resolution comparative map between the black muntjac (*M. crinifrons*) and the Chinese muntjac (*M. reevesi*,  $2n = 46$ ) has been constructed based on the chromosomal localization of 304 clones from a genomic BAC (bacterial artificial chromosome) library of the Indian muntjac (*M. muntjak vaginalis*,  $2n = 6♀/7♂$ ). In addition to validating the chromosomal homologies between *M. reevesi* and *M. crinifrons* defined previously by chromosome painting, the comparative BAC map demonstrates that all tandem fusions that have occurred in the karyotypic evolution of *M. crinifrons* are centromere–telomere fusions. The map also allows for a more detailed reconstruction of the chromosomal rearrangements leading to this unique and complex sex chromosome system. Furthermore, we have identified 46 BAC clones that could be used to study the molecular evolution of the unique sex chromosomes of the male black muntjacs.

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**Keywords:** BAC mapping; Chromosomal rearrangements; *Muntiacus crinifrons*; Tandem fusion; Sex chromosome system

Asian muntjacs (genus *Muntiacus*, family Cervidae) provide powerful models for studying karyotypic evolution and speciation because of their radical and rapid karyotypic diversification during the past 2 million years [1–4]. A tandem fusion hypothesis has been proposed to explain the karyotypic differences between Chinese muntjac (*M. reevesi*, MRE,  $2n = 46$ ) [5] and Indian muntjac (*M. muntjak vaginalis*,  $2n = 6♀/7♂$ ) [6,7]. This hypothesis is supported by both classical cytogenetic [8,9] and molecular cytogenetic studies [3,10–22]. Three types of tandem fusions could have occurred depending on the orientations of ancestral chromosomes involved: centromere–centromere fusion, telomere–telomere

fusion, and centromere–telomere fusion [9]. Comparative chromosome painting [14,17] and mapping of centromeric or telomeric repetitive DNA sequences [10–13] indicated that most, if not all, of the tandem fusions that have occurred during the karyotypic evolution of the extant muntjacs from a hypothetical  $2n = 70$  ancestral karyotype were centromere–telomere fusions [16,17,20]. This view is supported by architecture analysis of the fusion point [21] and comparative bacterial artificial chromosome (BAC) mapping in *M. reevesi* and *M. m. vaginalis* [22].

The black muntjac (*M. crinifrons*, MCR), endemic to a narrow region of the southeastern China [23], has a karyotype of  $2n = 8♀/9♂$  [24,25]. Previous chromosome painting studies [3,17,18] demonstrated that despite the diploid chromosome number of *M. crinifrons* being close to that of *M. m. vaginalis*, the genomic organization of the

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Table 1  
Summary of BAC clones mapped on the chromosomes of *Muntiacus reevesi* (MRE) and *Muntiacus crinifrons* (MCR)

MCR	MRE	Clone
1p	17	01H6, 04D9, <b>06G5</b> , <b>07A9</b> , <b>09E3</b> , 10F2, 54P15, 54P20, 55C8, 56A19, 58B18, 58C16
1p	8	<b>06D3</b> , 06E3, <b>09A2</b> , 09D5, 09E5, 53A19, 56B10, 58B17
1q	18	01B9, 01F10, <b>04D6</b> , 06A1, <b>06A4</b> , 09E2, 56D15, 58C17
1q	5a	06A6, 06D6, 06E2, <b>07B7</b> , <b>09B7</b> , 56B11, 58A4, 58C5, 58C7
1q	19	01F6, 06H3, <b>07B8</b> , <b>09A5</b> , 54O2, 55C7, 55O2, 58B24
1q	9	<b>06B3</b> , 07D12, <b>07E12</b> , 09E9, 10F4, 53A9, 53B8, 55B13, 55B16, 58B19, 58C6
1q	16	09E1, <b>09F8</b> , 54A11, 55A8, <b>55B17</b>
1q	21	01A2, 01H3, <b>06G4</b> , <b>07A8</b> , 09G12, 10E4, 10E7, 10E12, 54B22
1q	6	01E7, 06A2, 06C7, 06D8, <b>06F2</b> , <b>07A10</b> , 09D2, 09E2, 09E4, 54M16, 55A8, 56E11
1q	5b	<b>01B12</b> , 01D6, 04B9, 06F7, <b>07E5</b> , 09D6, 54F23, 56E3, 57A12
2p	7	06C10, 07B12, <b>07C8</b> , <b>07C12</b> , 54M14, 55A2, 55A3, 56E5, 56E21, 58B5
2q	10	<b>04F9</b> , <b>05A1</b> , 06B6, 06C5, 06C11, 09C7, 09D4, 09F1, 09G4, 09G8, 09H8, 10E5, 56A3, 56D4, 56D14, 56D21, 58B1, 58B8, 58B14
2q	11a	<b>01B3</b> , <b>06D10</b> , 53A4, 53A5, 53A6, 53A7, 53A10, 53B7, 55A7
2q	11b	<b>05A2</b> , <b>06E8</b> , 10E11, 53A3
2q	15	<b>06B12</b> , <b>07E7</b> , 54B12, 58B21, 58C4
2q	13	<b>01A1</b> , 01B1, 04H2, 06C4, <b>09A1</b> , 09B6, 09F4, 10F8, 56E1
2q	14	<b>04B2</b> , <b>06A5</b> , 09D12, 10E8, 56A16, 58A5, 58B22
2q	2b	04G2, 06G6, 09A9, <b>09A10</b> , <b>09B9</b> , 09F3, 54C1, 56E7
2q	2c	04D11, <b>05A5</b> , 06B2, 06H5, 07C7, <b>07D3</b> , 56D18
2q	2d	01D11, 01E3, 06E11, <b>06G10</b> , <b>07B5</b> , 07C4, 07D9, 10F5
3q	2a	<b>01A8</b> , 01D5, <b>07C6</b> , 09B10, 09C9, 54J24, 55A6, 56A5
3q	20	01A4, <b>01A11</b> , 06B7, <b>06C8</b> , 06D5, 07B1, 07D10, 07D11, 53A23, 58C1
3q	4b	01H4, 04D3, <b>04D4</b> , 05A8, 06F3, <b>07C5</b> , 07E11, 09D7, 53A1, 54N5, 55A4, 56A15, 56D20, 56E8, 58C13
3q	4c	01E6, <b>07A11</b> , <b>07D7</b> , 07E8, 09B5, 57A7
3q	1b	01A3, <b>01B4</b> , 01B11, 01F12, 04C1, 04H1, 06H9, <b>07D1</b> , 09G5, 10E2, 54E8
3q	1c	01D9, <b>07B9</b> , <b>07C10</b> , 09G2, 10E3, 54L3, 55A1, 58A1, 58A2, 58B2
(X+4)X	X	<b>01A7</b> , <b>01D10</b> , <b>07D6</b>
(X+4)q	3b	06B8, <b>06D1</b> , 07B3, <b>07C11</b> , 09D7, 54A21
(X+4)q	1a	01H12, <b>04A7</b> , <b>06A7</b> , 53A21, 58C21
(X+4)q	3a	<b>06D9</b> , 09B9, <b>09G6</b> , 53A17, 53B17, 54B3, 56B1
(X+4)q	4a	05A6, 06B5, <b>06G7</b> , <b>07B10</b> , 09C12, 53A16, 53P15, 58A16, 58B23
(X+4)q	22	04C6, 06D2, <b>06D11</b> , 09A12, <b>09B11</b> , 09B12
(X+4)q	12	06B4, <b>07E9</b> , <b>07E10</b>
(X+4)q	3c	04D5, <b>05A3</b> , 06A3, <b>06F1</b> , 09A6, 53B13, 54O19, 54P19, 55C13, 55B8, 56A4
(X+4)q	3d	<b>01B8</b> , 01B10, 01E5, 06C3, <b>07B11</b> , 09A7, 09B1, 09B2, 09E11, 09G3, 09H4, 09H6, 54N16, 55B4, 55C12, 56A11, 58C9
(1p+4)p	17b	<b>07A9</b> , 54P15, 56A19, 55C8, 10F2
(1p+4)p	22a	<b>06D11</b>
(1p+4)p	4a	05A6, 06B5, <b>06G7</b> , <b>07B10</b> , 09C12, 53A16, 53P15, 58A16, 58B23
(1p+4)p	3a	<b>06D9</b> , <b>09G6</b> , 53A17, 09B9, 53B17, 54B3, 56B1
(1p+4)p	1a	01H12, <b>04A7</b> , <b>06A7</b> , 53A21, 58C21
(1p+4)p	8	<b>06D3</b> , 06E3, <b>09A2</b> , 09D5, 09E5, 53A19, 56B10, 58B17
(1p+4)q	3b	06B8, <b>06D1</b> , 07B3, <b>07C11</b> , 09D7, 54A21
(1p+4)q	17a	01H6, 04D9, <b>06G5</b> , <b>09E3</b> , 54P20, 58B18, 58C16
(1p+4)q	22b	<b>04C6</b> , 06D2, 09A12, <b>09B11</b> , 09B12
(1p+4)q	12	06B4, <b>07E9</b> , <b>07E10</b>

Table 1 (continued)

MCR	MRE	Clone
(1p+4)q	3c	04D5, <b>05A3</b> , 06A3, <b>06F1</b> , 09A6, 53B13, 54O19, 54P19, 55C13, 55B8, 56A4
(1p+4)q	3d	<b>01B8</b> , 01B10, 01E5, 06C3, <b>07B11</b> , 09A7, 09B1, 09B2, 09E11, 09G3, 09H4, 09H6, 54N16, 55B4, 55C12, 56A11, 58C9
Yq	Yq	07D6

Boldface indicates those BACs shown in Fig. 2.

two species differs considerably. More interestingly, the male *M. crinifrons* has a sex chromosome system of X1X2Y1Y2Y3 that comprises approximately half of the entire genome [25]. Subsequent chromosome painting studies have shown that the X1, X2, Y1, Y2, and Y3 correspond to chromosomes X+4, 1, Y, 1p+4, and 1q of *M. crinifrons*, respectively [3,18]. Such a complex sex chromosome system, which originated within the past 0.5 million years [4], is unparalleled in other eutherian mammals so far studied. However, due to the inability of chromosome painting to resolve intrachromosomal rearrangements, the orientations of conserved segments as well as the detailed rearrangements leading to the unique Y2 (MCR 1p+4) in male *M. crinifrons* remain a puzzle [18].

Here we have developed a comparative BAC map between *M. crinifrons* and *M. reevesi* based on the chromosomal assignment of 304 BACs from the *M. m. vaginalis* library. The map refines the segmental homologies between *M. reevesi* and *M. crinifrons* established previously by comparative painting, demonstrating that the tandem fusions underpinning karyotypic evolution in *M. crinifrons* are exclusive centromere–telomere fusions. The results have also enabled the reconstruction of the pathway leading to the *M. crinifrons* chromosome 1p+4 (i.e., Y2), which, in a sense, represents a neo-Y chromosome.

## Results and discussion

Previous cytogenetic studies on muntjacs have predominantly focused on the *M. reevesi* and *M. m. vaginalis* because of the extreme karyotypic differences ( $2n = 46$  in *M. reevesi* while  $2n = 6/7$  in *M. m. vaginalis*) and wide availability of experimental materials. In contrast, the other muntjac species with equally interesting karyotypes [3,18] have been poorly studied. Here, 304 BAC clones containing unique DNA sequences derived from an *M. m. vaginalis* library have been assigned comparatively onto the chromosomes of *M. crinifrons* and *M. reevesi* (Table 1). The chromosomal localizations of all BACs are summarized on a high-resolution idiogram of *M. reevesi* (Fig. 1). A comparative BAC map between *M. crinifrons* and *M. reevesi* was constructed based on the chromosomal localizations of these BACs in both species (Fig. 2), which provides valuable information on the karyotypic evolution of *M. crinifrons*. Of the BACs mapped so far in *M. crinifrons*, 194 have also been mapped previously to *M. reevesi* and *M. m. vaginalis* [22].

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