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Chromosomal polymorphisms involving telomere fusion, centromeric inactivation and centromere shift in the ant *Myrmecia (pilosula) n = 1*

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Abstract. Detailed karyological surveys of the ant *Myrmecia pilosula* species group, which is characterized by the lowest chromosome number in higher organisms ($2n=2$), were attempted. We revealed that this species has developed highly complicated chromosomal polymorphisms. Their chromosome numbers are in the range $2n=2$, 3, and 4, and six polymorphic chromosomes are involved, i.e., two for chromosome 1 (denoted as SM_1 and ST_1), three for chromosome 2 (A_2, A_2', and M_2), and $M_{(1+2)}$ for the $2n=2$ karyotype. We suggested that these chromosomes were induced from a pseudo-acrocentric (A_1^M) and A_2 as follows: (1) $A_1^M \rightarrow SM_1$ or ST_1 by two independent pericentric inversions; (2) $A_2 \rightarrow A_2' \rightarrow M_2$ by chromosomal gap insertion and centromere shift; and (3) $ST_1 + A_2 \rightarrow M_{(1+2)}$ by telomere fusion, where (3) means that the $2n=2$ karyotype was derived secondarily from a $2n=4$ karyotype. It is a noteworthy finding that active nucleolus organizer (NOR) sites, in terms of silver staining, are tightly linked with the centromere in this species, and that both the centromere and NOR of A_2 were inactivated after the telomere fusion.

Introduction

The ant *Myrmecia pilosula* (Fr. Smith) is one of the most primitive formicids in Australia, and is commonly called the 'Jack-jumper', due to its hopping behaviour. Although this species has long been considered as a single biological species (Clark 1954; Brown 1953), we found several years ago that it is a cytologically heterogeneous species, involving $2n=9$, 10, 31 and 32 chromosome forms (Imai et al. 1977). More recently, a unique '*pilosula*' colony having the lowest chromosome number in higher organisms ($n=1$ in males and $2n=2$ in workers) has been discovered by Crosland and Crozier (1986).

Encouraged by these findings, we have started an international cooperative programme aimed at a karyological and taxonomic survey of *M. pilosula*. Large-scale field studies were carried out in 1985 and 1987. During these surveys more than 150 '*pilosula*' colonies were collected from New South Wales, the Australian Capital Territory (A C T), Victoria, South Australia, and Tasmania.

It was revealed by these surveys that the chromosome numbers of *M. pilosula* range more divergently than previously thought, i.e., $2n=2$, 9, 10, 15, 17–32 (Crosland et al. 1988; Imai et al. 1988a). As there are some significant but subtle morphological variations as well as karyological differentiation, it is now clear that *M. pilosula* is a complex species including at least five separate but similar biological species. Details will be published elsewhere. We deal here with chromosomal polymorphisms in the species currently denoted *M. (pilosula) n = 1*, and discuss the origin of the karyotype with the lowest chromosome number in higher organisms ($n=1$).

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Materials and methods

The materials used here were named temporarily *Myrmecia (pilosula) n = 1* by R.W.T. (Imai et al. 1988a). *M. (pilosula) n = 1* is distinguished from other members of the *pilosula* group by its stocky form and details of cuticular sculpture and pilosity. It builds a small flat nest mound, with no pebbles on the mound. A total of 11 colonies have been collected from Canberra (A C T) (HI87-165, 235), the Mongarlowe/Charleyong district (N S W) (HI87-136, 148, 150, 151, 153, 154, 157), South Warrandyte (Vic.) (HI87-213), and Tidbinbilla (A C T), where HI87 is the code number (H. Imai, 1987). The Tidbinbilla colony was collected by M. Crosland in 1985. It was later sent to Japan and has been subsequently cultured by H.T.I. The colonies HI87-151, 165, and 235 are also being bred by H.T.I. at the National Institute of Genetics for C-banding and nucleolus organizer region (NOR) analysis.

Chromosomal preparations were made using cerebral ganglia of prepupa by the improved air-drying technique (for details see Imai et al. 1988a). The preparations were stained with Giemsa (3% in M/15 Sørensen's pH 6.8 phosphate buffer) for 10 min at room temperature. For the NOR silver staining, we followed the method of Howell and Black (1980). A brief outline of the technique is as follows: Two chemicals are used: (A), a 50% solution of $AgNO_3$, and (B), a gelatin solution with formic acid (50 ml distilled water:1 g gelatin:0.5 ml formic acid). Both solutions should be prepared freshly and filtered through a 0.22 μm Millipore filter. After observing the chromosomes first by Giemsa staining, the preparation is put into absolute glacial acetic acid for 10 min to remove the Giemsa completely. Six drops of solution (B) are added to the preparation with a 1 ml disposable syringe and then 3 drops of solution (A). Both solutions are mixed completely by flipping the slides, and covered with a fine nylon mesh

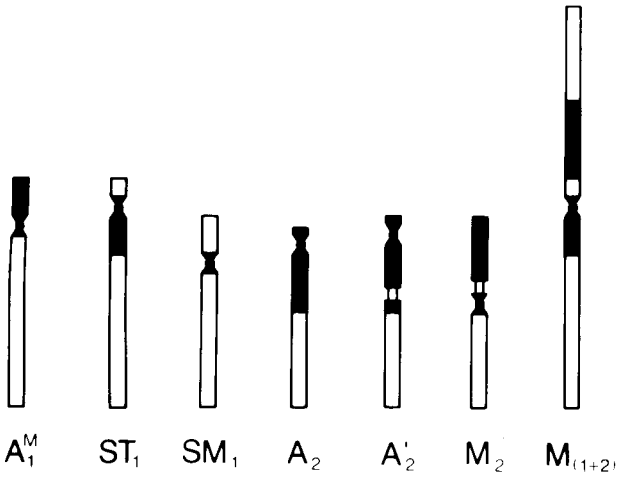

Fig. 1. Schematic representation of polymorphic chromosomes observed in *Myrmecia (pilosula)* $n=1$ and abbreviations of their nomenclature. Chromosome 1: A_1^M a (hypothetical) acrocentric chromosome with extraordinarily elongated heterochromatic short arm (=pseudo-acrocentric); ST_1 a subtelocentric chromosome derived from A_1^M by a pericentric inversion; SM_1 a submetacentric chromosome derived from A_1^M by a pericentric inversion. Chromosome 2: A_2 an acrocentric chromosome with a large heterochromatin block at the proximal region of the long arm; A_2' an acrocentric chromosome derived from A_2 by a chromosomal gap insertion; M_2 metacentric with a totally heterochromatic short arm derived from A_2' by a centromere shift. Chromosome 1 and chromosome 2: $M_{(1+2)}$ a large metacentric chromosome found in the $n=1$ karyotype resulting from a telomere fusion between ST_1 and A_2

(2.5×3 cm^2). The preparation is heated in a steamer (water bath) at 73° C for 3.5 min. After cooling the preparation to ca. 40° C in air, the nylon mesh and the precipitated silver particles are removed with running tap-water, and the slide allowed to dry completely. Best results are obtained if fresh preparations (within 1 day) are used.

As the chromosomal polymorphisms found in *M. (pilosula)* $n=1$ are extremely complicated, in the present text we use the following abbreviations of the chromosomal nomenclature:

A_1^M, ST_1, and SM_1 for chromosome 1
A_2, A_2', and M_2 for chromosome 2
$M_{(1+2)}$ for the $2n=2$ karyotype.

For details see Figure 1.

For the same reason, we formulate polymorphic karyotypes of this species following terminology 'K' devised by Imai and Crozier (1980). For example, the diploid karyotype with one pair of $M_{(1+2)}$ chromosomes is represented $2K=2M_{(1+2)}$ (Fig. 2a), and that having one pair of SM_1 and one pair of A_2' is formulated $2K=2SM_1+2A_2'$ (Fig. 2h).

Results

Chromosomal polymorphism in M. (pilosula) n=1

The *pilosula* colony which was first found at Tidbinbilla (near Canberra) showed a homomorphic karyotype, i.e., one pair of large metacentrics ($2K=2M_{(1+2)}$ in our nomenclature) (Crosland and Crozier 1986; Imai et al. 1988a). Our present observations revealed, however, that this ant species has a chromosome number variation. Diploid chromosome numbers were observed in the range $2n=2$, 3, and 4 (Table 1). Among ten colonies examined, three colonies had homomorphic karyotypes for either $2n=2$ (HI87-151 and 157) or $2n=4$ (HI87-165). The other ones showed heterogeneous chromosome numbers; $2n=2$ or 3 (HI87-148, 150, 153, and 213), $2n=3$ or 4 (HI87-136 and 154), and $2n=2$ or 3 or 4 (HI87-235). For details, see Figures 2 and 3. As each individual had its own stable chromosome number ($2n=2$ or 3 or 4), this chromosome number variation does not result from the so-called B-chromosome.

All of the $2n=2$ karyotypes comprise one pair of large metacentrics (Fig. 2a), but those having $2n=3$ or 4 are

Table 1. Karyological data of *Myrmecia (pilosula) n=1*

Colony codes (HI87-)	No. of chromosomes $2n$	No. indivisual observed	Modal cell no. observed	Diploid karyotype (2K)
136	3	8	160	$1M_{(1+2)}+1SM_1+1M_2$
136	4	7	128	$2SM_1+2M_2$
148	2	1	20	$2M_{(1+2)}$
148	3	9	180	$1M_{(1+2)}+1SM_1+1M_2$
150	2	5	84	$2M_{(1+2)}$
150	3	5	90	$1M_{(1+2)}+1SM_1+1M_2$
151	2	9	180	$2M_{(1+2)}$
153	2	1	20	$2M_{(1+2)}$
153	3	5	100	$1M_{(1+2)}+1SM_1+1M_2$
154	3	3	60	$1M_{(1+2)}+1SM_1+1M_2$
154	4	3	60	$2SM_1+2M_2$
157	2	3	30	$2M_{(1+2)}$
165	4	1	20	$2SM_1+2A_2'$
165	4	5	100	$2SM_1+1A_2+1A_2'$
213	2	3	60	$2M_{(1+2)}$
213	3	7	140	$1M_{(1+2)}+1SM_1+1A_2$
235	2	3	60	$2M_{(1+2)}$
235	3	3	60	$1M_{(1+2)}+1ST_1+1A_2'$
235	4	8	170	$1ST_1+1SM_1+2A_2'$

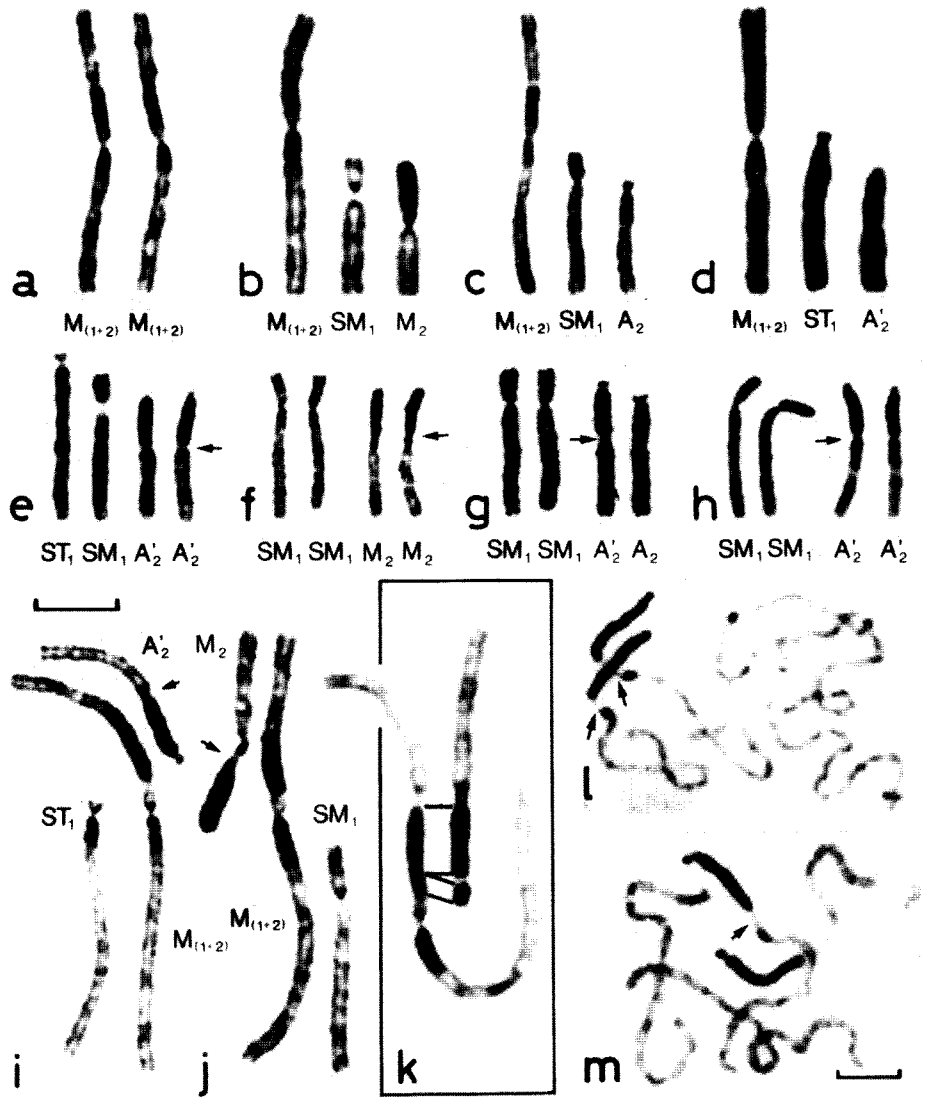

Fig. 2a–m. Diploid karyotypes (2K) in *Myrmecia (pilosula) n=1*. **a** $2n=2$, **b–d** $2n=3$, **e–h** $2n=4$. The polymorphic karyotypes are formulated as follows: **a** $2K_1=2M_{(1+2)}$, **b** $2K_2=1M_{(1+2)}+1SM_1+1M_2$, **c** $2K_3=1M_{(1+2)}+1SM_1+1A_2$, **d** $2K_4=1M_{(1+2)}+1ST_1+1A'_2$, **e** $2K_5=1ST_1+1SM_1+2A'_2$, **f** $2K_6=2SM_1+2M_2$, **g** $2K_7=2SM_1+1A'_2+1A_2$, and **h** $2K_8=2SM_{(1+2)}+2A'_2$. Early prometaphase karyotypes with C-banding of $2K_4$, $2K_2$ and $2K_3$ are represented in **i**, **j**, and **k**, respectively. *Arrows* indicate chromosomal gaps inserted in A'_2. **l** and **m** show individuals homozygous and heterozygous for the chromosomal gap of A'_2, respectively. Bars represent 5 μm

highly heterogeneous in components. As is shown in Figure 2b–h, three types of $2n=3$ karyotypes and four types of $2n=4$ karyotypes can be discriminated. To describe these complicated karyotypes more simply, we will take the $2n=4$ karyotype shown in Figure 2h as the standard.

The karyotype shown in Figure 2h is comprised of one pair of submetacentrics (SM) and one pair of acrocentrics with a secondary constriction (denoted as A′; see arrow in Fig. 2h). We define SM and A′ as chromosome 1 and chromosome 2, respectively, and represent them by SM_1 and A'_2. In Figure 2e, the homologues of chromosome 2 are homomorphic ($2A'_2$), but those of chromosome 1 are heteromorphic, i.e., one is the SM_1 mentioned above and the other is subtelocentric. The subtelocentric is termed here ST_1. The example in Figure 2g, the karyotype has $2SM_1$, but chromosome 2 is heteromorphic. One of the two is A'_2; the other is acrocentric, but there is no secondary constriction. We denote it A_2 to discriminate it from A'_2. The karyotype shown in Figure 2f has $2SM_1$, but chromosome 2 is metacentric with a secondary constriction (see arrow), like A'_2. It is named M_2. By these definitions, two types of chromosome 1 (SM_1 and ST_1) and three types of chromosome 2 (A_2, A'_2 and M_2) are discriminated in $2n=4$ karyotypes (Figs. 1 and 2). These ST_1, A_2, A'_2, and M_2 chromosomes are characterized by a large heterochromatin block at the pericentromeric region or in their short arms (see the black column in Fig. 1). We also use the term $M_{(1+2)}$ for the large metacentric found in $2n=2$ or 3 karyotypes (see below).

By using $M_{(1+2)}$, SM_1, ST_1, A_2, A'_2 and M_2 as defined above, the eight unique diploid karyotypes (2K) shown in Figure 2a–h (temporarily abbreviated here as $2K_1$, $2K_2$, ..., $2K_8$) are formulated as follows:

$2n=2$: $2K_1=2M_{(1+2)}$ (Fig. 2a)
$2n=3$: $2K_2=1M_{(1+2)}+1SM_1+1M_2$ (Fig. 2b)
$2K_3=1M_{(1+2)}+1SM_1+1A_2$ (Fig. 2c)
$2K_4=1M_{(1+2)}+1ST_1+1A'_2$ (Fig. 2d)
$2n=4$: $2K_5=1ST_1+1SM_1+2A'_2$ (Fig. 2e)
$2K_6=2SM_1+2M_2$ (Fig. 2f)
$2K_7=2SM_1+1A_2+1A'_2$ (Fig. 2g)
$2K_8=2SM_1+2A'_2$ (Fig. 2h)

The $2K_1$ and $2K_2$ karyotypes were the two dominant types, with 33.7% for the former and 28.1% for the latter. The

relative frequencies of $M_{(1+2)}$, SM_1, M_2, A'_2, A_2 and ST_1 were 69.7%, 60.7%, 44.9%, 19.1%, 13.5%, and 12.4%, respectively.

Homology of the polymorphic chromosomes

The six types of polymorphic chromosomes found in *M. (pilosula) n=1* are classified into the three categories of $M_{(1+2)}$, chromosome 1 (SM_1 and ST_1), and chromosome 2 (A_2, A'_2 and M_2) (Fig. 1). The homology of A_2, A'_2 and M_2 can be concluded from the cytological evidence that homomorphic SM_1 chromosomes are shared by the $2K_6$ ($=2SM_1+2M_2$), $2K_7$ ($=2SM_1+1A_2+1A'_2$) and $2K_8$ ($=2SM_1+2A'_2$) karyotypes. As mentioned in the previous section, we called these SMs chromosome 1, and represented them as SM_1 (Fig. 2f–h). The other pairs (denoted as $2M_2$, $1A_2+1A'_2$, and $2A'_2$ in Fig. 2f–h) fall therefore into the category of chromosome 2, in spite of their morphological heteromorphism. In chromosome 2, A'_2 was probably induced from A_2 by insertion of a chromosomal gap near the distal end of the large heterochromatin block in the long arm (Fig. 4). Such a secondary constriction was observed more clearly in early prometaphases, e.g., Figure 2l for $2A'_2$ and Figure 2m for $1A_2+1A'_2$ (see arrows). The same chromosomal gap was observed also in M_2 (Fig. 2f and j). The only difference between A'_2 and M_2 is the location of the centromere. The centromere is near the terminal in A'_2, but it is at the heterochromatin-euchromatin junction in M_2. In the same manner, the karyotype $2K_5$ ($=1ST_1+1SM_1+2A'_2$) (Fig. 2e) indicates that ST_1 is homologous with SM_1 (i.e., chromosome 1).

The homology between the large $M_{(1+2)}$ and the other chromosomes (especially SM_1, A'_2, and M_2) seemed mysterious (Fig. 2b, c and j). Important information for solving this question was obtained, however, from the $2K_4$ karyotype ($=1M_{(1+2)}+1ST_1+1A'_2$) (Fig. 2d). In this karyotype, the long arm of ST_1 matches exactly with that of $M_{(1+2)}$, and the short arm of ST_1 with the small euchromatin block adjacent to the centromere in the short arm of $M_{(1+2)}$ (Fig. 2i). In the same manner, A'_2 corresponds to the large heterochromatin block and the distal euchromatin in $M_{(1+2)}$ (see Fig. 2i). There is no visible difference in the size of the large heterochromatin block in $M_{(1+2)}$ and that of A_2 except for a chromosomal gap due to the primary constriction in A_2 (Fig. 2k). This series of observations suggests strongly that $M_{(1+2)}$ was induced by a terminal fusion between the short arm tips of ST_1 and A_2, which was termed 'telomere fusion' by Imai et al. (1988b). For this reason, we denoted the large metacentric chromosome as $M_{(1+2)}$.

Close linking of the centromere and active NOR site in M. (pilosula) n=1 chromosomes

As a marker for discriminating chromosomal mutations, we observed active NOR sites by the silver-staining technique (Howell and Black 1980). The active NOR sites of $M_{(1+2)}$, ST_1, SM_1, A'_2 and M_2 are demonstrated in Figure 3e–i, respectively. It is a noteworthy characteristic that all of these chromosomes have one active NOR site in their primary constriction at metaphase. The chromosomal configurations at anaphase of $2K_1$ ($=2M_{(1+2)}$), $2K_2$ ($=1M_{(1+2)}+1SM_1+1M_2$), $2K_4$ ($=1M_{(1+2)}+1ST_1+1A'_2$), and $2K_8$ ($=2SM_1+2A'_2$) karyotypes are represented in Figure 3a–d. Note that there is an exact correspondence between the 'centromere' as an initiative centre for polar moving at anaphase and the primary constriction at metaphase. This means, in other words, that the centromere and the active NOR site are always linked tightly in *M. (pilosula) n=1*, as well as in *Tapinoma* (Palomeque et al. 1988).

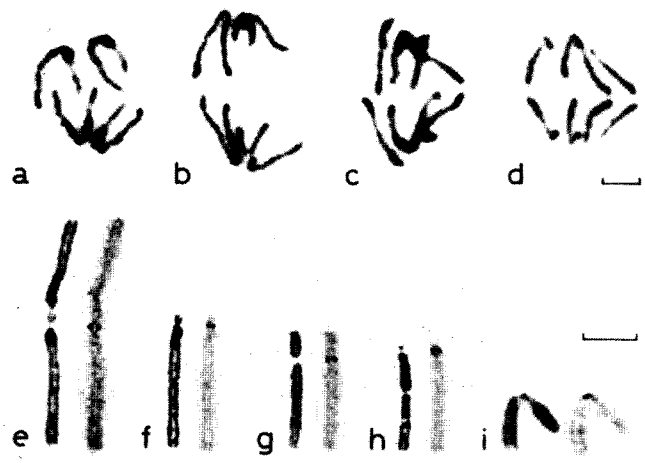

Fig. 3a–i. Chromosomal configurations at anaphase (**a–d**) and active nucleolar organizer region (NOR) sites observed by means of silver staining (**e–i**). **a** $2K_1=2M_{(1+2)}$. **b** $2K_2=1M_{(1+2)}+1SM_1+1M_2$. **c** $2K_4=2M_{(1+2)}+1ST_1+1A_2$. **d** $2K_8=2SM_1+2A'_2$. **e** $M_{(1+2)}$. **f** ST_1. **g** SM_1. **h** A'_2. **i** M_2. Bars represent 5 μm

Discussion

We have shown above that *M. (pilosula) n=1* has developed highly complicated chromosomal polymorphisms involving at least six morphologically distinctive chromosomal types, i.e., SM_1 and ST_1 for chromosome 1, A_2, A'_2 and M_2 for chromosome 2, and $M_{(1+2)}$ (Figs. 1 and 2). We wish to discuss here the idea that the series of polymorphic chromosomes was differentiated from a hypothetical karyotype which is represented temporarily as K_0 and may be formulated $2K_0=2A_1^M+2A_2$. Of these $2K_0$ chromosomes, A_2 was actually observed in $2K_3$ ($=1M_{(1+2)}+1SM_2+1A_2$) and $2K_7$ ($=2SM_1+1A_2+1A_2$) (Fig. 2c and g). On the other hand, A_1^M is a hypothetical chromosome (Fig. 1), which has been named a 'pseudo-acrocentric' by Imai et al. (1988a), i.e., an acrocentric with an extraordinarily elongated heterochromatic short arm. Starting from $2K_0=2A_1^M+2A_2$, at least three series of independent chromosomal alterations would have occurred in this species (Fig. 4). A brief outline follows.

The first series of alterations occurred in chromosome 1 (SM_1 and ST_1) (Fig. 4, bottom row). We could not find any possible chromosomal alterations which induce either $SM_1 \rightarrow ST_1$ or $ST_1 \rightarrow SM_1$. The only reliable possibility may be that both SM_1 and ST_1 were derived from A_1^M by two independent pericentric inversions. We could not find A_1^M in this *n=1* form, unfortunately, but such chromosomes are frequently found in other *pilosula* forms, especially in the group named 'black head' (e.g., see Figs. 8 and 9 in Imai et al. 1988a).

We suggested in the previous section a unidirectional alteration changing $A_2 \rightarrow A'_2 \rightarrow M_2$ for chromosome 2 (Fig. 4, top row). The induction of A'_2 from A_2 is easily interpreted by a chromosomal gap insertion. However, the

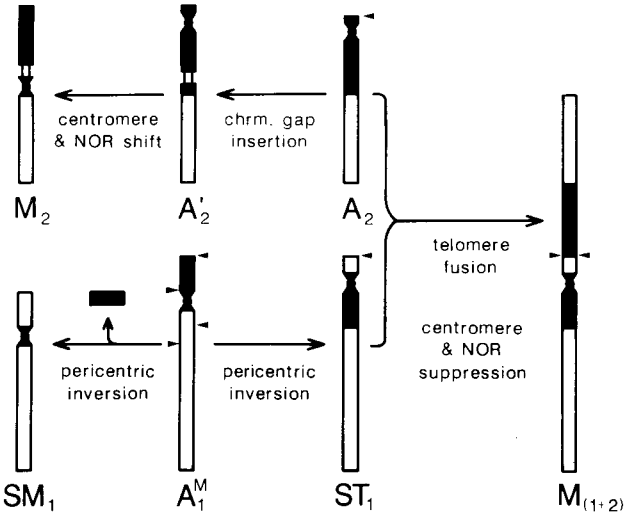

Fig. 4. A scheme for chromosomal alterations in *Myrmecia (pilosula) n=1*. *Solid circles* at the primary constrictions represent active NOR sites. *Arrowheads* indicate loci where chromosomal mutations were assumed. The A_1^M chromosome is a hypothetical acrocentric chromosome with an extraordinarily elongated heterochromatic short arm (=pseudo-acrocentric). For details see text

next alteration ($A_2' \rightarrow M_2$) seems to be somewhat unusual. In A_2' and M_2 the size of the heterochromatin and the location of the chromosomal gap are exactly the same (Figs. 1 and 2). The only difference between them is the location of the centromere and NOR (Fig. 3). The topological pattern of the chromosomal gap precludes the chromosomal alteration from A_2' to M_2 or the reverse by a simple pericentric inversion. The only possible solution seems to be a centromere shift from the terminal of A_2' to the euchromatin-heterochromatin junction of M_2. If we accept this assumption, we have to assume a shift of the active NOR site also, because there is no active NOR site in the subterminal region of the heterochromatic short arm of M_2 which corresponds to the primary constriction of A_2 (compare Fig. 3h and i).

The third event is concerned with the origin of $M_{(1+2)}$. Based on the C-banding patterns of $2K_4$ ($=1M_{(1+2)}+1ST_1+1A_2'$) (Fig. 2i), we concluded that $M_{(1+2)}$ was induced by the so-called telomere fusion which occurred at the short arm terminals of ST_1 and A_2' (see Fig. 4, arrowheads). The centromere and NOR of $M_{(1+2)}$ obviously originated from those of ST_1 (compare Fig. 3e and f). If this interpretation is correct, we have to assume inactivation of the centromere and NOR in the short arm of $M_{(1+2)}$, which is homologous with A_2 or A_2' (Figs. 2i, 3e, h and 4).

Many cases of centromeric inactivation following telomere fusion have been reported recently in mammals (for details see Imai 1988; Imai et al. 1988b). We have found the same phenomenon in the ant *Ponera scabra*, and also centromeric 'reactivation' in *Myrmecia (piriventris) HI85-302* (Imai et al. 1988a). These observations suggest that the inactivation of the centromere and NOR found in $M_{(1+2)}$ of *M. (pilosula) n=1* is not an unacceptable assumption. The M_2 induction by the centromere and NOR shift mentioned above may be another example of inactivation and reactivation of the centromere and NOR, although we need further supporting evidence at the molecular level.

So far as our observations are concerned, the most simple but reasonable interpretation for the karyotypic alterations in *M. (pilosula) n=1* may be that its ancestral karyotype was $2K_0=2A_1^M+2A_2$ (i.e., $2n=4$), and the lowest karyotype, $2K_1=2M_{(1+2)}$ having $2n=2$, was derived secondarily from a hypothetical karyotype $2K'=2ST_1+2A_2'$ by telomere fusion between ST_1 and A_2, as summarized in Figure 4.

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