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).

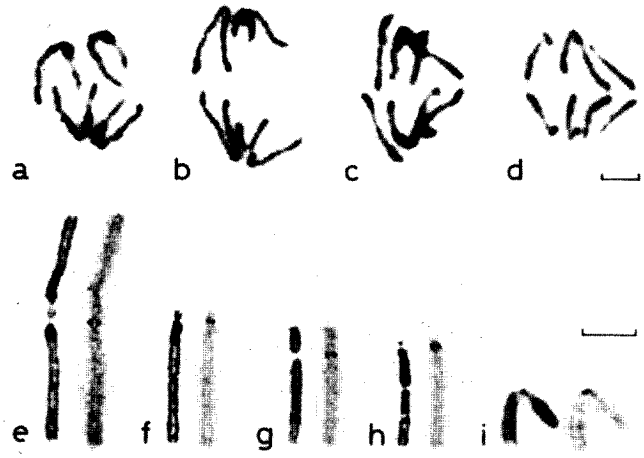

Fig. 3a–i. Chromosomal configurations at anaphase (**a–d**) and active nucleolar organizer region (NOR) sites observed by means of silver staining (**e–i**). **a** $2K_1=2M_{(1+2)}$. **b** $2K_2=1M_{(1+2)}+1SM_1+1M_2$. **c** $2K_4=2M_{(1+2)}+1ST_1+1A_2$. **d** $2K_8=2SM_1+2A'_2$. **e** $M_{(1+2)}$. **f**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