increased nutrient uptake. It will also make the plant more resistant to pathogens as a result of increased PRO and PPO activities. The present investigation suggests that AM inoculation would help in re-establishment and conservation of this endangered tree of the Indian Thar desert. Use of AM fungi as a fertilizer helps in the establishment of plants in arid and semiarid regions and also in the increase of fertility of soil by making available phosphorus and nitrogen to the plant. Use of AM fungi as a biofertilizer is a low-cost technique, but results are surprisingly better than the use of chemical fertilizers. So, these results open new prospects on the utilization of AM fungi.

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Meiotic XY association could be both chiasmate and achiasmate in the Indian pygmy field mouse, *Mus terricolor*

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Between the two alternative hypotheses explaining the nature of meiotic XY association in male mammals, chiasmate and achiasmate, only the former has gained credence. XY bivalents at diakinesis/metaphase-I in the Indian pygmy field mouse *Mus terricolor* make cytological visualization of chiasma feasible, due to the accretion of a block of heterochromatin distal to the pseudoautosomal region. The results revealed that meiotic XY association in *M. terricolor* could be either chiasmate or achiasmate, suggesting that the latter could also ensure successful meiotic progression.

MEIOSIS is the process whereby ploidy is maintained over generations in sexually reproducing organisms. In mammals with XY sex determination system in the males, maintenance of the association between the X and Y chromosomes is essential for survival of the meiocytes to form gametes[1], barring exceptional species where the X and Y chromosomes do not associate in meiotic prophase-I. The X and Y chromosomes share a segment of genetic homology, the pseudoautosomal region (PAR), that has the potential to undergo homologous synapsis and reciprocal recombination. However, the cytological manifestation of reciprocal exchange, i.e. chiasma, is generally not seen in a majority of mammals, including the mouse; and the X and Y chromosomes are seen associated end-to-end at diakinesis/metaphase-I. This association is variously interpreted as 'obligate chiasmate'[2,3] or 'achiasmate'[4] association. Presently, there is a strong

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inclination in favour of the obligate (obligatory) chiasmate hypothesis[1]. Studies in sex-reversed XY^{Sxr} mouse in which part or all of the short arm of the Y chromosome has been duplicated and transposed to the distal tip of the long arm beyond the PAR[5,6] and in mouse carrying Y* rearrangement (Y* chromosome is a product of translocation of a functional centromere and associated major satellite sequences from an unknown chromosome to a terminal position distal to the PAR of the Y chromosome; the normal Y centromere is either inactivated or deleted[7]) suggest that an obligate single crossover between the X and Y chromosomes is a prerequisite for completion of meiosis[3,7]. The high rate of X–Y dissociation at diakinesis/metaphase-I observed in XY^{Sxr} and XY* mouse, resulting from recombination-failure[3,7,8], leads to reduced testis weight due to cell death[7,9]. While no distinct chiasma has been observed between the X and Y chromosomes in normal male mouse, there is some cytological evidence for a terminal chiasma[3].

The X and Y chromosomes in the Indian pygmy field mouse, *Mus terricolor*, that is closely related to the house mouse, are distinct in the subgenus *Mus* due to accretion of heterochromatic blocks forming a large p-arm in the X chromosome and an enlarged acrocentric Y chromosome (see figure 1 in ref. 10). Furthermore, the terminal ends of the long arms of both the X and Y chromosomes bear a GC-rich, C-band positive heterochromatic block, distal to the pseudoautosomal region[11] (Figure 1 *a*). This means that should the XY bivalent have an obligate chiasmate association, a chiasma will be visible at diakinesis/metaphase-I in which the GC-rich heterochromatic block would make the homologous chromatids distal to the chiasma.

We analysed diakinesis/metaphase-I stages in *M. terricolor*, to examine the obligate occurrence of chiasma between the X and Y chromosomes. A total of 152 diakinesis nuclei were observed from three male mice. Only 42 nuclei (27.6%) showed a clear chiasmate association between the X and Y chromosomes; 57 nuclei (37.5%) had end-to-end associated XY and 37 nuclei (24.3%) had dissociated X–Y. The nature of the XY association remained unclear in the rest of the nuclei. When chiasmate, as expected, the distal heterochromatic blocks in the long arms of the X and Y chromosomes formed the homologous chromatids distal to the chiasma (Figure 1 *b*). Conversely, in the end-to-end associated condition, no chromatin was observed distal to the association point of the XY, even in nuclei with extended bivalents, suggesting that this association could be achiasmatic (Figure 1 *c*).

The end-to-end XY association at diakinesis/metaphase-I, however, gave rise to a few possibilities.

1. A chiasma could form proximal to the GC-rich heterochromatic block, but its terminalization limits cytological resolution.
2. Differential condensation of the distal heterochromatic block interferes with visualization of chiasma.
3. A terminal chiasma could form between the distal heterochromatic blocks of the X and Y chromosomes.
4. Both chiasmate association[2,3] and nonchiasmate end-to-end association[4] could occur.

Differential labelling of sister chromatids by *in vivo* BrdU incorporation during premeiotic S-phase provided evidence that chiasma does not terminalize in animals investigated such as grasshopper, hamster and mouse[12,13], in the light of which chiasma terminalization is now considered as an untenable dogma[14]. We do not consider the second possibility as valid, since a clear chiasmate association (with an 'open centre') was visible even in condensed XY bivalents in which the distal heterochromatic blocks were still recognizable as a minute segment distal to the chiasma. On the contrary, when a chiasma was not visible, the distal heterochromatic blocks were in clear end-to-end association even in bivalents that were fairly extended (compare the right bivalent in Figure 1 *b* with the left one in Figure 1 *c*). Given the general lack of chiasma in heterochromatic segments, the third possibility also looks less likely.

Periodic acid-Schiff stained histological section of testis in *M. terricolor* has shown[15] that the ratio between primary spermatocytes and round spermatids in stage VII of spermatogenesis ranges from 1 : 2.4 to 1 : 3.6. This means that out of every four products of a single meiosis, 0.4 to 1.6 cells died before reaching the spermatid stage (every primary spermatocyte produces four spermatids upon completion of two meiotic divisions). Intriguingly, though X–Y dissociation at diakinesis/metaphase-I was frequent, sex chromosome aneuploidy was never observed in metaphase-II[16]. Together, these data could be taken to suggest that the spermatocytes that failed to maintain XY association till diakinesis/metaphase-I had perished before reaching metaphase-II, in *M. terricolor*.

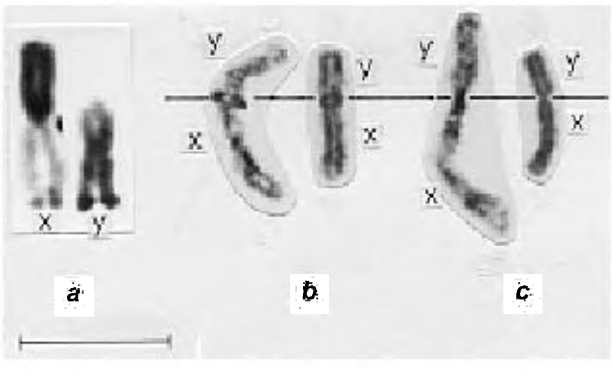

Figure 1. Cut-outs of X and Y chromosomes in *M. terricolor* (***a***) C-banded mitotic X and Y chromosomes. Arrows indicate the distal heterochromatic blocks in the long arms of both X and Y chromosomes. Chiasmate (***b***) achiasmate end-to-end associated (***c***) XY bivalents at diakinesis. Bivalents on the left in both (***b***) and (***c***) are less condensed; and those on the right are more condensed. Note that chiasma is still visible in the condensed bivalent in (***b***) Bar = 10 μm.

That XY chiasmate association occurs in mouse is amply evident, though earlier it has never been observed. The distal blocks of heterochromatin in *M. terricolor* have made the XY chiasma clearly visible. But, more importantly, it has led to the realization that true nonchiasmate terminal association between the X and Y chromosomes[4] could be possible, even in species that forms XY chiasma (as in *M. terricolor*). Since the faithful progression of meiosis ensures maintenance of ploidy in sexually reproducing organisms, the features that increase fidelity of the meiotic divisions would be favoured by selection. It is therefore likely that to reduce the cost of meiotic subversion, two diverse mechanisms have evolved to secure the maintenance of XY association during meiotic first division which in turn would ensure cell survival.

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MEETINGS/SYMPOSIA/SEMINARS

Short-Term Course on Electrophoresis Techniques

Date: 13–18 May 2002
Place: Yercaud

Topics include: Theory and practicals on various electrophoresis techniques employed routinely in biological sciences. Paper/agarose gel electrophoresis (PAGE) of proteins, DNA; Immunoelectrophoresis; isoelectrifocusing; 2D PAGE; DNA sequencing; Blotting techniques and gel documentation. Participants are limited to 20 only.

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