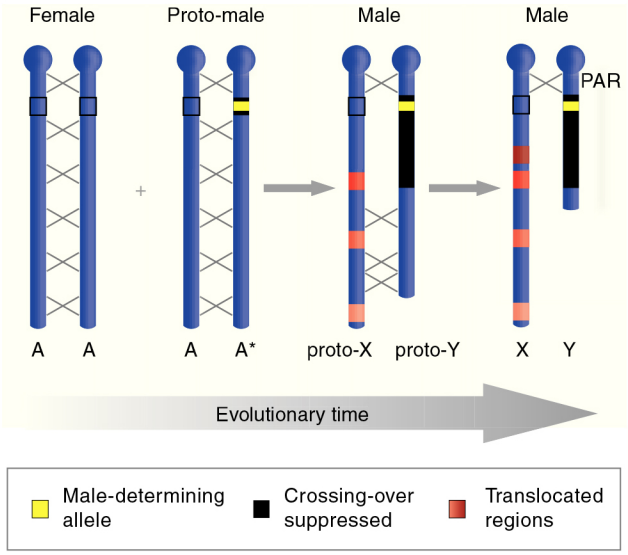

Figure 1. Evolution of the Y chromosome. Early in evolution, the two sexes may have differed at only a single, autosomal locus (marked by a black box); one sex is homozygous at this locus (female) and the other sex (male) is heterozygous (designated proto-male). The "male-determining allele" is shown in yellow. If mating requires one member of each sex, then individuals homozygous for the male-determining allele cannot arise. At this early stage, physiological differences between the sexes will be subtle, comparable to those that distinguish the two mating types in yeast. To prevent the formation of intersex states, crossing-over will be suppressed within and around the male-determining locus (dark shading). Mutations, including deletions and inversions, will accumulate and cause the degenerate region in which crossing-over is suppressed to gradually expand ("Muller's ratchet") until the chromosome has lost most of its active, functional genes. (Mutations accumulate because suppression of crossing-over reduces the probability that they will occur in homozygous form, hence, reducing the selection pressure against them.) A small, active region must remain that is homologous to the X chromosome to allow pairing and crossing-over at meiosis (indicated by a gray ×). This is the pseudoautosomal region (PAR). The autosome, originally homologous to the future X (A in the diagram), will itself evolve sometimes through translocations from other chromosomes (shown as red shaded areas), eventually forming the distinctive X chromosome. The X, like other chromosomes, is a mosaic of DNA fragments put in place at different periods through evolution; some of these are ancient and some are relatively recent. On the human X, the more recent arrivals are enriched in genes that escape X inactivation.