

Figure 1
Litomosoides sigmodontis karyotype. Aceto-orcein stained spermatozoa from the seminal receptacle of an adult female worm, showing five or six condensed chromosomes (arrowed).

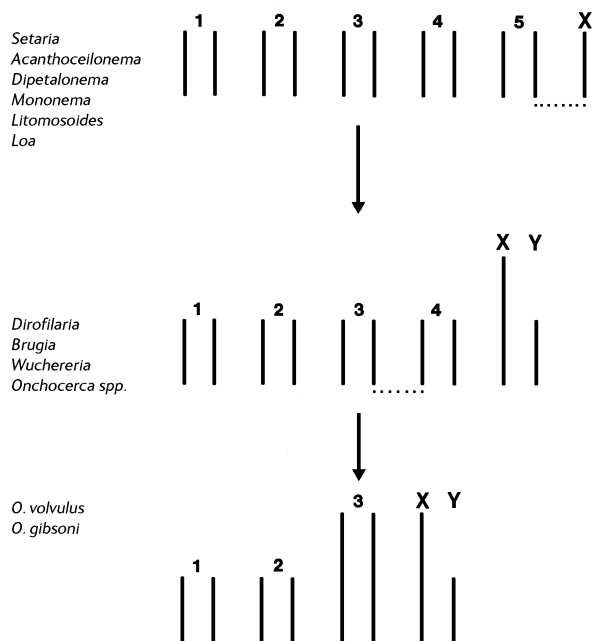


Figure 2
Karyotype evolution in the Filariidae.

as each other, whereas in the 4A+XY species the four autosomes and the Y-chromosome are of comparable size, whereas the X-chromosome (which would be an X-autosome fusion product) is visibly larger. The 3A+XY karyotype observed in *O. volvulus* and *O. gibsoni* is likely to have been derived from the 4A+XY karyotype by a fusion between two autosomes [12]. The relative sizes of the different chromosomes are consistent with this hypothesis in

that one of the autosomes is clearly the largest chromosome, and presumably the autosome-autosome fusion product.

The pattern of karyotype evolution (Figure 2) is likely to reflect organismal evolution and indicate taxonomic relationships. All species of filarioids which have been examined for their chromosomes are from the family Onchocercidae, and from three subfamilies, Setariinae (*Setaria* spp), Dirofilarinae (*Dirofilaria* and *Loa*) and Onchocercinae (all other species in Table 1). The presumed ancestral state (5A+X0) occurs in the Setariinae, most of the Onchocercinae and *Loa loa* (but not *Dirofilaria*). Current phylogenetic opinion has been unable to resolve the major clades of the Onchocercinae, which reduce to a star polytomy [28]. *Loa* forms a clade from this unresolved polytomy, but *Dirofilaria* is consistently grouped along the *Onchocerca* clade. The reduction to 4A+XY has occurred in both *Dirofilaria* and *Onchocerca*, and hence it supports the molecular data, but it also indicates that the *Onchocerca/Dirofilaria* clade is most closely related to the *Wuchereria/Brugia* clade because it is found in both.

The observation that *O. volvulus* apparently shares the same karyotype as *O. gibsoni*, but not *O. ochengi* or *O. dukei*, might be taken as evidence for a close phylogenetic relationship, and Muller [29] also considered that *O. volvulus* was most closely related to *O. gibsoni* on the basis of the structure of the cuticle. However, Bain [30] held that *O. volvulus* was taxonomically more closely related to *O. ochengi*, and recent molecular phylogeny reconstruction using the 12s, 16s and ND5 mitochondrial genes very strongly supports this view (Morales Hojas, Cheke and Post, unpublished data). If this is true, it would indicate that the similar karyotypes of *O. volvulus* and *O. gibsoni* have been produced by two different fusion events (which may not even have involved the same pairs of autosomes), and this is likely to be reflected in the precise position of the translocation breakpoints at the molecular level.

B-chromosomes and nucleolus organising region

Both *O. volvulus* and *O. gibsoni* have B-chromosomes [12,14]. These are supernumerary chromosomes which are not present in every individual, and when they are present they can be haploid, diploid, triploid, tetraploid, etc, in different individuals. The origin and subsequent evolution of B-chromosomes is a long-standing problem in genetics [31]. B-chromosomes can have definite phenotypic effects, but it has always been unclear whether this was the result of specific genes or a mere consequence of the presence of an extra chromosome. It is largely unknown whether B-chromosomes carry genes and whether those genes are repeated elsewhere in the more constant part of the genome. In any case, if the origin of