feature of nematode development. In *C. elegans* it is clear that there is a fixed number of cell divisions (including post-embryonic cell divisions) during development leading to a constant number of somatic nucleii in the adult [6]. This is not true of *R. culicivorax* where the number of somatic nucleii varies and is correlated with adult size [7]. There have been no specific studies of these patterns in Filariae, but Bain [8] has reported somatic cell divisions in developing larvae of *O. volvulus* in the vector. Furthermore, counts of lacto-acetic orcein stained nucleii [9] of intrauterine microfilariae and infective L3 larvae of *O. volvulus* have indicated a mean of 280 nucleii in microfilariae and approximately 900 in L3s [10]. It is clear that the concept of eutely can not be applied to filariae, because there is obviously an increase in cell number between these two post-embryonic stages. It is also unlikely that filariae have a fixed number of cell divisions because larvae at the same stage of development were found to show variation in numbers of somatic nuclei [9].

It seems that most nematodes probably have holocentric chromosomes (the chromosomes attach to the meiotic and mitotic spindle microtubules along their whole length, instead of this function being concentrated into a single centromere) [11]. A consequence of this is that broken fragments of chromosomes can still assort regularly at cell division. However, it is clear that the trichurids (at least) have normal (localised) centromeres, but the situation is not well understood for the filariae. Procunier and Hirai [12] interpreted their mitotic and meiotic metaphases from *O. volvulus* and *O. gutturosa* in terms of localised centromeres, but it is not obvious that their drawn figures are correct interpretations of their photographs, and they explained that "the position of the centromere is not always obvious" and in the longest chromosome its position "appears to vary between individuals". The chromosomes of the filariae are very small, difficult to interpret and no other authors have directly addressed this issue. However, the orientation of the chromosomes at metaphase has been remarked upon. Delves et al. [13] showed that synaptonemal complexes were present in early female meiosis of *Dirofilaria immitis*, but at metaphase I the chromosomes appeared to be pairing end to end. This was particularly obvious for the X chromosome pair (which is the longest chromosome in *D. immitis*) because a more normal side by side pairing was observed in only 10% of ova. This same end to end pairing is apparent in the photographs of other authors for other filariae (for example [14]). In most animals meiotic metaphase chromosomes show evidence of crossing over (which is the visible manifestation of recombination), but this is not obvious for filariae. Procunier and Hirai [12] interpreted their figures to show crossing over, but no other authors have done so, and it is not clear whether this is due to the small size of the chromosomes or some more fundamental biological reason. In any case, recombination is expected to occur in filariae because they have synaptonemal complexes [13] and recombination has been proven in some other nematodes such as *Caenorhabditis* [15], and *Globodera* [16].

Some nematodes such as *Strongyloides* exhibit forms of parthenogenesis, and a few such as *Mermis subnigrescens* have environmental sex determination (dependant upon the number of mermithids parasitising a particular insect host). However, amongst the vertebrate parasites chromosomal sex determination seems to be the rule. And there seems to be an X0 system in all species where it is known except the Oxyuridae (which have a system of haplo-diploidy), Ascaridae (which have multiple sex chromosomes) and Filarioidea (where some species of Onchocercidae have an XY system). It is clear that the X0 system is fundamental to nematodes (including the filariae), and the few XY systems which occur amongst the filariae are secondary derivatives. In other organisms with X0 sex chromosomes, such as Orthoptera, the fusion of an autosome to the X chromosome to create a neo-XY is very well documented [17]. Genetically, an X0 sex determining system has to be a 'balance' system, and there is a good understanding of the molecular basis of sex determination in *Caenorhabditis* (which has an X0 system, with X0 males and XX hermaphrodites) [18], and it is probable that filariae are basically similar.

Chromosome numbers and karyotype evolution

Table 1 summarises all published records of filarial karyotypes, and there are apparently three basic types, 5A+X0, 4A+XY and 3A+XY. There are a few exceptions in the literature, and it is not always clear the extent to which these might be errors resulting from the difficult nature of filarial chromosomes, or indicative of natural variation. *Litomosoides sigmodontis* has been reported to have either 5A+X0 (new unpublished data, see Figure 1) or 4A+X0 [19,20]. In view of the karyotypes of other X0 species it is likely that 5A+X0 is correct, and 4A+X0 is either the result of natural variation for an autosome-autosome translocation or a mistake (due to small difficult chromosomes). Indeed, there are clearly six chromosomes present in some of McLaren's [20] illustrations. Similarly Taylor [19] reported *Dirofilaria immitis* to have 4A+X0, whilst other authors reported 5A+X0 [20] or 4A+XY [21,13]. It is possible that this reflects natural variation within *Dirofilaria*, but Taylor [19] did not have access to a past body of published work that later cytogeneticists have been able to build upon, and it seems most likely that 4A+X0 was a mistake. Post et al. [22] reported that *Onchocerca tarsicola* from Germany was 4A+XY (i.e. n = 5), but the same species from Sweden was n = 3. This difference was attributed to possible intraspecific geographic variation. Most authors agree that *O. volvulus* has 3A+XY (i.e. n = 4).