The separate identities of the male-determining factor, \( M \), and the sex-linked \textit{Distorter} gene, \( D \), are established in an Accra strain of \textit{Aedes aegypti}. Their positions in the Y chromosome are defined in relation to each other and to Giemsa C-bands. Thus, \( M \) is invariably inherited with the centromere, whereas \( D \) lies towards the intercalary band. Approximately 1.2% recombination occurs between \( M \) and \( D \) but, in a chromosome known for its distal localization of chiasmata, it is argued that the two are not necessarily as closely linked cytologically as this might imply. Evidence on the genetic effects of recombination in the region of \( M \) and \( D \) is also considered.

Introduction

In certain strains of the mosquito, \textit{Aedes aegypti} (L.), sex-ratio distortion in favour of males is clearly due to paternal meiotic drive (Craig et al., 1960, 1961; McClelland, 1960; Wood, 1961; Hickey & Craig, 1966a, b). Affected males, heterozygous for the male-determining 'gene' \( M \) linked with the \textit{Distorter} gene \( D \), transmit a disproportionate number of \( MD \)-bearing Y chromosomes to their progeny, irrespective of the female genotype. The expression of \( D \) is determined by the degree of sensitivity or resistance of the homologous X chromosome (Wood, 1976), there being six levels of X chromosome sensitivity, \( m^{s1} \) to \( m^{s6} \), and two of resistance, \( m^{r1} \) and \( m^{r2} \), which can be recognized by the sex ratio of the progeny (Wood, 1976; Suguna et al., 1977), the last producing a slight excess of females.

It is well known that the sex locus, \( M \) or \( m \), is situated towards the centre of the genetic linkage map of chromosome 1 (Craig & Hickey, 1967; Bhalla & Craig, 1970), which is the shortest of the three chromosomes (Bhalla, 1973), and cytological studies have shown that it is also invariably inherited with the median centromere (Newton et al., 1974). Moreover, there is genetical evidence to suggest that the \textit{Distorter} gene is similarly closely linked with the male determining gene or genes (Hickey & Craig, 1966a, b). However, the reliability of the central portion of the linkage map of this chromosome is severely limited by distal localization of crossing-over in the sex bivalent (Newton et al., 1976).

The present paper is concerned with defining the relative positions of \( M \) and \( D \) more precisely than has so far been possible. For this purpose, use has been made of the cytological markers provided by Giemsa C-banding. Thus, an X chromosome is banded in the region of the centromere and in an intercalary position about half way along one arm, whereas a Y chromosome never shows a centromeric band, although it may possess an intercalary band. Advantage has also been taken of the fact that metaphase-I of meiosis in distorting \((MD/m^{s+})\) males is disturbed and involves X chromosome breakage (Newton et al., 1974, 1976), by means of which meiotic drive can be identified cytologically.

Material and methods

Two laboratory strains of \textit{A. aegypti} have been studied.

Chipei: derived from larvae collected by Dr. J.C. Lien on the island of Chipei (Taiwan) in June 1973.

Accra: derived from larvae collected in Accra (Ghana) in July 1973 and supplied by Dr. W.Z. Coker.

The Chipei strain has no driving Y chromosomes.
but its X chromosomes are highly sensitive \((m^2d)\) to distortion and all possess both an intercalary and a centromeric C-band (Newton et al., 1974, 1976). The Accra strain includes a high proportion of driving Y chromosomes without intercalary C-bands and, although its X chromosomes are polymorphic in their sensitivity, all possess both bands.

The structure and behaviour of Chipei and Accra X chromosomes in the presence of Y chromosomes derived from the polymorphic Accra strain have been studied throughout the breeding programme outlined in Figure 1. All rearing techniques were identical to those described by Wood (1976).

Mitosis in third or fourth instar larval brains, and meiosis in pupal testes, were both examined in cytological squash preparations. Some were Feulgen stained but most were treated by the Giemsa C-banding technique used previously (Newton et al., 1974).

**Results**

Although there is some variation in their size, intercalary C-bands appear to be universally present in X chromosomes of the Accra strain (Fig. 2a-f), a similar range occurring in approximately 11.6% of Y chromosomes (Fig. 2d,e). The remaining 88.4% of Y chromosomes are completely unbanded (Fig. 2f) and their high frequency has been used as a means of interpreting the events of male meiosis during the course of the experiment outlined in Figure 1.

Since crossing-over proximal to the intercalary C-band is very rare (Newton et al., 1974), it is possible to infer the probable Giemsa C-band constitution of the Y chromosome of a parental male by examining a sufficiently large sample of his F1 progeny. As expected, a random sample of 216 F1 males taken from 35 of the 45 single pair crosses between Chipei females and Accra males (Fig. 1) revealed both banded and unbanded Y chromosomes but each type was almost exclusively confined to particular families. Thus, a band was totally absent from the Y chromosomes examined in 30 families (Fig. 3) but was invariably present in another (family 2) (Fig. 4). However, families 1, 14, 15 and 36 were heterogeneous (Figs. 5 & 6) with a low frequency of banded Y chromosomes, the simplest explanation for which is recombination as a result of crossing-over between the two bands.

Most sex ratios in the F1 generation were not distorted but where distortion did occur it varied in degree. In fact, the F1 generation indicated the presence, not only of driving Y chromosomes in Accra, but also of X chromosomes differing in their sensitivity to drive. Progenies consisting of 8.22% females \((\chi^2 = 50.97; P < 0.001)\) and 17.98% females \((\chi^2 =