The Embryonic Organization of the Genital Disc Studied in Genetic Mosaics of *Drosophila melanogaster*

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Summary. The embryonic organization of the sexually dimorphic genital disc was studied in genetic mosaics resulting (a) from early loss of a chromosome or (b) from mitotic recombination.

(a) *Early Loss of a Chromosome*. Three types of mosaics were produced—purely female mosaics, purely male mosaics, and gynandromorphs. They show that the genital disc arises from a group of cells in the ventral region of the embryo somewhat larger than that giving rise to a single foreleg (Table 2). Within this group of cells three regions can be distinguished that are present in both sexes: an anterior, a medial, and a posterior one, with distances of only 3–4 sturts between adjacent regions. The anterior region gives rise to the female genitalia, the medial region to the male genitalia, and the posterior region forms the analia of both sexes and the parovaria of the female (Figs. 2 and 3). The relative positions of the three regions were deduced from sturt distances (Tables 1 and 5), and from frequencies of mosaicism (Table 2).

(b) *Mitotic recombination* was induced at the blastoderm stage in order to produce twin spots in the external genitalia and analia of purely male and female flies. Clone sizes indicate that these structures arise from a small number of precursor cells (Table 4). Clones overlapped right and left sides, but no clones were found extending over analia and genitalia. However, within either the analia or the genitalia of each sex, no clonal restrictions could be observed, and the clones comprised structures that were up to 12 sturts apart. A comparison of clone sizes and sturt distances in the foreleg and in the genital disc indicates that equal gynandromorph distances involve equal numbers of cells in different regions on the ellipsoid egg (Fig. 5).

The results obtained from all mosaics provide a consistent picture of the embryonic organization of the genital disc. This becomes apparent in the summarized fate maps (Fig. 4), where the map derived from normal

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gynandromorphs can be produced by a simple superposition of the male and the female maps. The data are also discussed with respect to mechanisms of sexual differentiation in the genital disc.

**Key words:** *Drosophila* — Gynandromorphs — Cell lineage — Sexual dimorphism — Genital discs.

**Introduction**

Determination and differentiation of sexual dimorphism represent a fundamental problem of developmental biology. The genital disc of *Drosophila* is especially well suited for studying the developmental parameters and the genetic control of sexual development. The derivatives of this imaginal disc show a complete sexual dimorphism such that all adult structures formed by the disc in a female are different from those formed in a male. This sexual dimorphism is already apparent in the genital disc at the end of the second larval instar (Laugé, 1969), and thus the fundamental processes of sex determination leading to morphological differences must have taken place before that time. In order to study how sexual dimorphism arises in the course of development, a detailed description of the initial organization of the precursor cells in the embryo is necessary. In particular, it is important to determine whether only one group of cells gives rise to both male and female structures, or whether these structures derive from two different regions in the embryo. In the first case, sexual determination for each cell involves a choice between two patterns, in the second case a decision whether or not to develop into adult structures. From studies of gynandromorphs with mosaic genital discs, Nöthiger et al. (1977) have proposed that the former mechanism governs the development of the anal plates, the latter that of the genitalia. One of the aims of this investigation was to test this hypothesis in pure males and females.

Our experiments have been directed towards the following specific questions:

- What is the number of precursor cells at the blastoderm stage that will give rise to the genital disc, and how are these cells arranged?
- Is there a difference between the fate maps derived from male and female flies, and how do these maps compare with that derived from sexually mosaic gynandromorphs?
- What are the cell lineage relationships in the primitive genital disc?
- How do clone sizes relate to sturt distances in the posterior region of the egg as compared to the thoracic region?

Since the disc precursors cannot be identified in the early embryo, we decided to study their development indirectly in genetic mosaics. Purely female mosaics, purely male mosaics and gynandromorphs were generated by the loss of an unstable chromosome. They were used to determine the relative sizes of the precursor areas for different adult structures and the relative distances between them. This information was summarized in embryonic fate maps of the genital discs. A second category of genetic mosaics was generated by mitotic recombination. These mosaics allowed us to estimate the absolute number of precursor