S8

The experimental demonstration of compartments in *Drosophila*

The segment compartments are carried over into the imaginal discs that derive from specific segments (see Fig. 2.6), and into the adult structures, such as wings and legs, that derive from the imaginal discs (discussed in Chapter 10).

Cell-lineage restriction within compartments is most clearly illustrated by the behavior of cells in the wing of the adult fly. It is easier to distinguish lineage restriction in adult structures than in embryonic and early larval structures, because in adults there has been considerable cell division since the initial event that determined the compartment in the embryo. Techniques such as those described below (see Section S9 online on genetic mosaics and mitotic recombination) showed that in a normal wing the compartment boundary is remarkably sharp and straight and does not correspond to any structural features in the wing (Fig. S8.1).

Compartments were first defined by making genetically mosaic flies composed of two distinguishable kinds of cells (see Section S9 online). Single cells in the embryonic blastoderm or in the larval epidermis are given a distinctive phenotype by X-ray-or laser-induced mitotic recombination. The fates of all the descendants of this marked cell are then followed. Their behavior depends on the stage of development at which the founder nucleus was marked. Descendants of nuclei marked at early stages during cleavage become part of many tissues and organs, but descendants of nuclei marked at the blastoderm stage or later have a more restricted fate. They are found only in the anterior or the posterior part of each segment (or of an appendage such as a wing), never throughout the whole segment.

Cells of imaginal discs divide only about 10 times after the cellular blastoderm state; thus clones of experimentally marked cells are small, even in the adult, and so it is not easy to detect a boundary of lineage restriction (see Fig. S8.1, top panel). Clone size can be increased by the *Minute* technique, which results in the marked cell dividing many more times than the other cells (see Section S9 online). A single clone of such cells can almost fill either the anterior or posterior part of the wing, and this makes the boundary that the cells never cross more evident: this boundary separates the anterior and posterior compartments (see Fig. S8.1, middle panel). These experiments also show that the pattern of the wing is in no way dependent on cell lineage. A single marked embryonic cell can give rise to about a twentieth of the cells of the adult wing or, using the *Minute* technique to increase clone size, about half the wing. The lineage of the wing cells in each case is quite different, yet the wing's pattern is normal. This indicates that what is being patterned in this case is groups of cells, rather than patterning occurring on an individual cell-by-cell basis. As we shall see in Chapter 6, this is very different from the situation in the nematode *C. elegans*, where the cell lineages in development are constant and the patterning occurs at the level of the identity of individual cells.

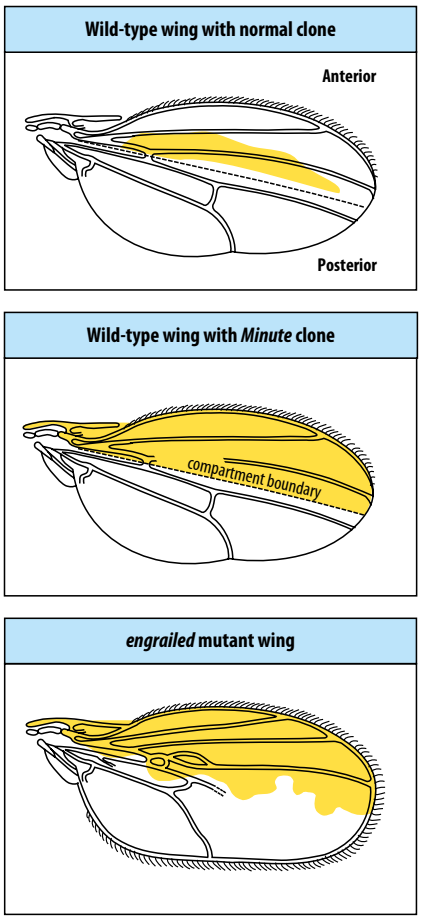

Fig. S8.1 The boundary between anterior and posterior compartments in the *Drosophila* wing can be demonstrated by marked cell clones. Top panel: in the wild-type wing, clones marked by mitotic recombination in the embryo, which gives marked cells a phenotype different from other cells of the wing, are too small to demonstrate the compartment boundary. Middle panel: the use of the *Minute* technique produces an increased rate of cell division in the marked cell and gives clones large enough to determine that cells from one compartment do not cross the boundary into an adjoining compartment. Bottom panel: in the wing of an *engrailed* mutant in which the engrailed protein is not produced, there is no posterior compartment or boundary. Clones in the anterior part of the wing cross over into the posterior region and the posterior region is transformed into a more anterior-like structure, bearing anterior-type hairs on its margin. As described earlier, the *engrailed* gene is required for the maintenance of the character of the posterior compartment, and for the formation of the boundary.

The specification of cells as the posterior compartment of a segment (the anterior of a parasegment) initially occurs when the parasegments are set up, and is due to the *engrailed* gene. Expression of *engrailed* is required both to confer a 'posterior segment' identity on the cells and to change their surface properties so that they cannot mix with the cells adjacent to them, hence setting up the parasegment boundary. Direct evidence for the role of *engrailed* comes from the behavior of clones of wing cells in an *engrailed* mutant (see Fig. S8.1, bottom panel). In the absence of normal *engrailed* expression, clones are not confined to anterior or posterior parts of the segment and there is no compartment boundary. Moreover, in *engrailed* mutants, the posterior compartment is partly transformed so that it comes to resemble the pattern of the anterior part of the wing. For example, bristles normally found only at the anterior margin of the wing are also found at the posterior margin.