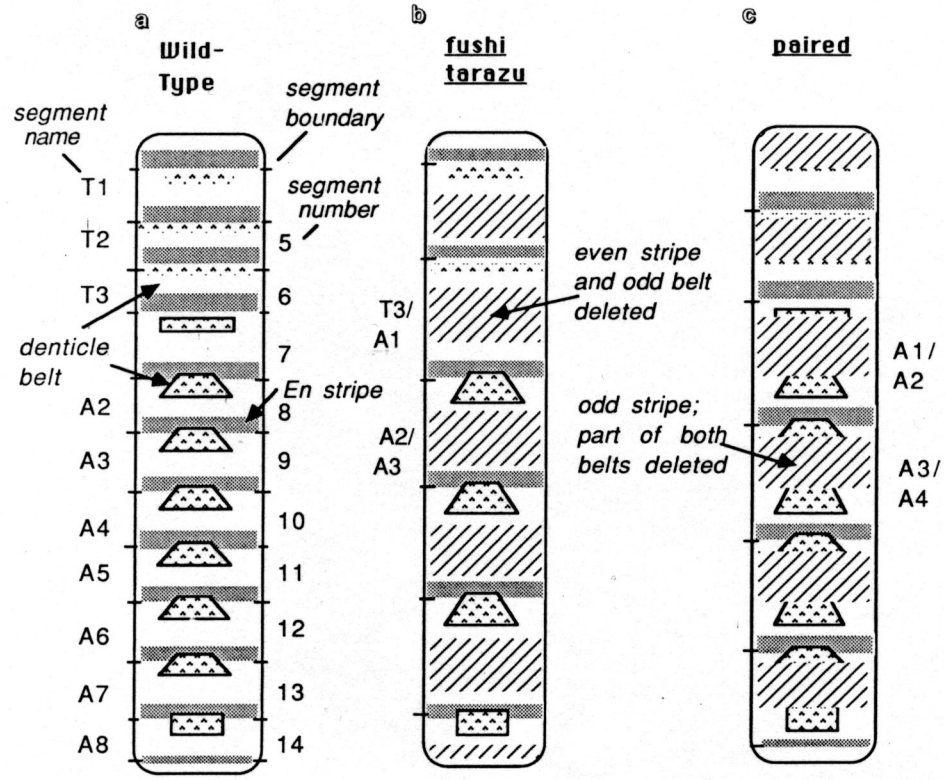

Figure 1. A schematic representation of the wild-type, *ftz*, and *prd* larval cuticle with the pattern of *engrailed* expression superimposed. (*a*) Selected ventral characteristics of a wild-type embryo at hatching. The thoracic (T1–T3) and eight abdominal (A1–A8) segments are externally visible; cuticular derivatives of the oral (Mn, Mx, La) segments, which have largely involuted, and the complex terminalia have been left out for clarity. The approximate positions of segment boundaries are marked (–). Note that this boundary actually lies just within the denticle belt of segments A2–A8 (Szabad et al. 1979). The T1–T3 and A1 denticle belts probably do not overlap this boundary. The posterior portion of each segment is comprised of mostly naked cuticle. The placement of the *engrailed* stripes is approximate. These overlap mostly naked cuticle and the anterior row of denticle hairs in A2–A8. This placement is derived from a consideration of the pattern elements lost in a weak *engrailed* mutant, en^{IM99} at 18°C (Gergen et al. 1986; S. DiNardo, unpubl.). (*b*) Pattern elements deleted in a *ftz* embryo. The regions deleted, indicated by crosshatching, extend from the middle of the naked cuticle in even-numbered segments through the next denticle belt, ending in the naked cuticle region of the adjacent odd-numbered segment, resulting in compound segments, e.g., T3/A1, A2/A3, etc. The remaining denticle belts are broadened relative to wild type. The frame of deletion should effect even-numbered *engrailed* stripes (see Fig. 2). (*c*) Pattern elements deleted in a *prd* embryo. The deletions are in a different frame from those in *ftz* embryos. The deletion takes out part of the denticle from belt and the naked cuticle of odd-numbered segments and part of the adjoining even-numbered denticle belt, resulting in compound segments, e.g., A1/A2, A3/A4. The composite denticle belts are broadened relative to wild type. The deletion frame should affect odd-numbered *engrailed* stripes (see Fig. 2).

that would derive from even-numbered *engrailed* stripes are absent in *ftz* mutants [e.g., 6(T3) in Fig. 1b]; whereas those that would derive from odd-numbered stripes are absent in *prd* mutants [e.g., 9(A3) in Fig. 1]. Some of this pattern deletion may be the result of cell death at later stages. Second, the mutants develop fused (compound) segments, having disproportionately wide denticle belts characterized by duplicated rows of denticles (reflecting an enlarged anterior compartment; Nüsslein-Volhard et al. 1985). Thus, beyond any cell death that might occur, some misspecification of cells occurs and appears to contribute to the final pattern.

The *ftz* and *prd* gene products do not act alone in the establishment of even- and odd-numbered *engrailed* stripes. Like *ftz* mutants, early *opa* embryos also lack even-numbered stripes (Fig. 3a), although after germband extension, there is some *engrailed* expression roughly corresponding to the location of even-numbered stripes (Fig. 3b). This expression is usually faint and clustered near the ventral midline. Interestingly, at these later stages the expression in odd-numbered stripes is sometimes irregular [5(T2), bold arrow, Fig. 3b]. Such late changes in *engrailed* pattern occur in many pair–rule mutants. We will describe in detail the late changes observed in one particular pair–rule mutant, *odd-skipped*, in a later section, and we will consider the implications of such late changes in the Discussion.

Like *prd* mutants, seven odd-numbered stripes are missing in *upd* mutant embryos (Fig. 3c). However, this phenotype is not fully penetrant. Twenty-five percent of the mutant embryos show this drastic and early effect on *engrailed* pattern. In the remaining mutant embryos,