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Review

Controlling cell shape changes during salivary gland tube formation in *Drosophila*

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ABSTRACT

Any type of tubulogenesis is a process that is highly coordinated between large numbers of cells. Like other morphogenetic processes, it is driven to a great extent by complex cell shape changes and cell rearrangements. The formation of the salivary glands in the fly embryo provides an ideal model system to study these changes and rearrangements, because upon specification of the cells that are destined to form the tube, there is no further cell division or cell death. Thus, morphogenesis of the salivary gland tubes is entirely driven by cell shape changes and rearrangements.

In this review, we will discuss and distill from the literature what is known about the control of cell shape during the early invagination process and whilst the tubes extend in the fly embryo at later stages.

Contents

1. Introduction

The embryonic salivary glands in the *Drosophila* embryo form from two specified patches of epithelial cells within the embryonic epidermis called placodes (Fig. 1A and C). The collective action of various homeotic transcription factors [TFs] (such as Homothorax [Hth], Extradenticle [Exd], Sex combs reduced [Scr]; [1,2]) and signalling molecules (such as Dpp; [3]) defines the two bilateral

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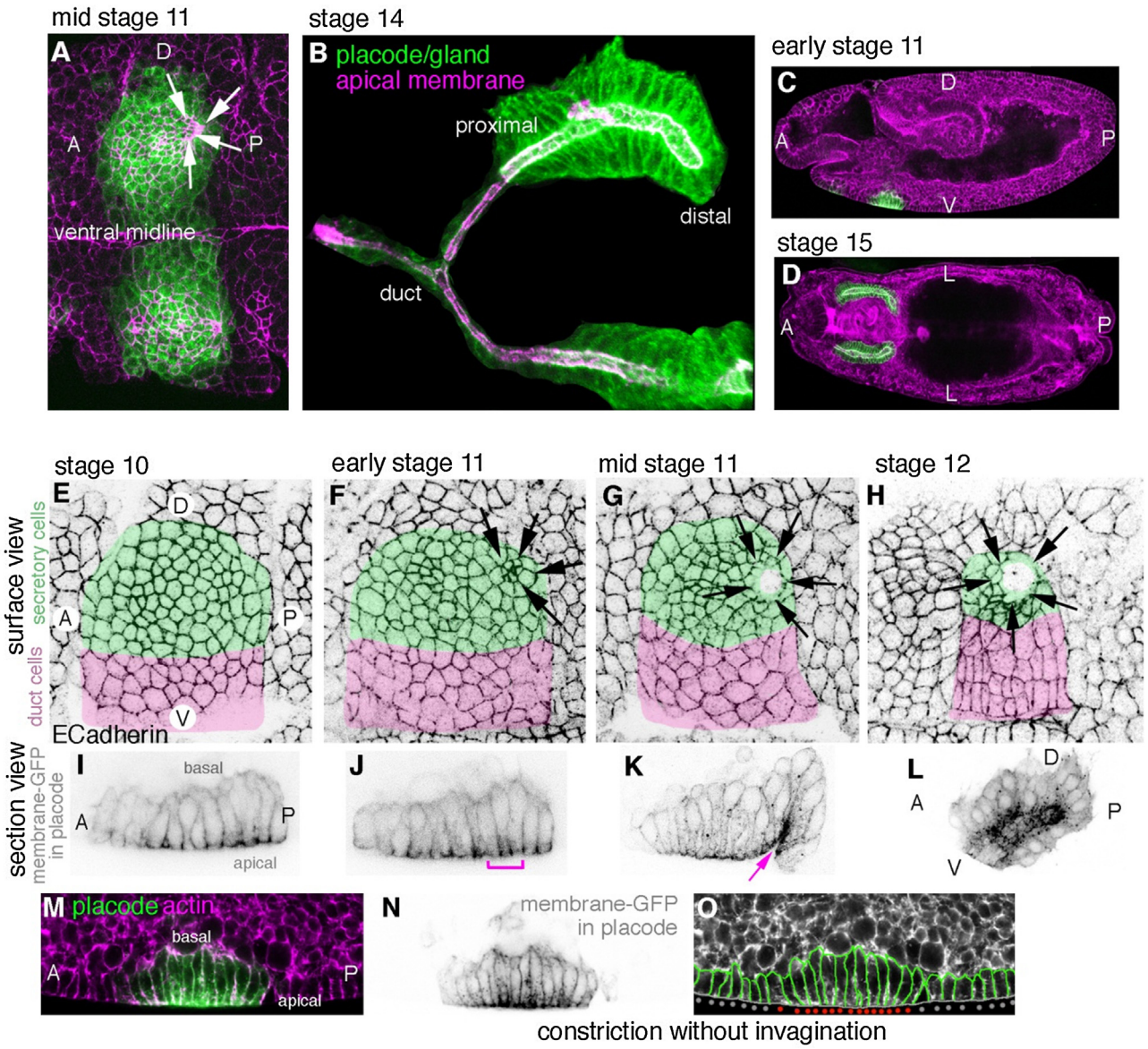

Fig. 1. Early apical constriction and invagination in the salivary gland placode. (A and B) The salivary glands form from two epithelial placodes (green in A) on either side of the ventral midline and invaginate through a focal point in the dorsal-posterior corner (arrows in A; surface view). By the end of stage 14 most cells have invaginated to form two secretory tubes linked at the proximal end by a Y-shaped duct (B). (C and D) Positioning of the early placode (C) and fully invaginated glands (D) within the embryo. The placode is genetically labelled with membrane-GFP in green in A–D, apical membrane is magenta in A and B, and actin is magenta in C and D. A–D are modified from Ref. [19]. (E–L) Apical cell shape changes during early constriction and tissue bending. E–H show surface views, I–L show corresponding section views. At stage 10 (E and I) apices within the placode have not yet constricted. At early stage 11, apices in the dorsal-posterior corner start to narrow (arrows in F, bracket in J), but no invagination is occurring yet. At mid stage 11 a small invaginating pit has formed (arrows in G, arrow in K). This pit extends into the invaginating tube as more cells constrict in a precise pattern across the placode (arrows in H). Apical surface in E–H is marked by E-Cadherin, secretory cells are indicated in pale green, duct cells in pale magenta, the plasma membrane of placodal cells in I–L is marked by membrane-GFP. M–O further illustrates the apical constriction without tissue bending observed at early stage 11. In contrast to surrounding cells (magenta in M) placodal cells (N, and green in M) have narrowed apices: each dot in O marks the centre of a cell apex: note that the density of red dots marking placodal cells is much higher than density of white dots in the surrounding epidermis. Embryo and gland orientation indicated by A (anterior), P (posterior), D (dorsal), V (ventral), L (lateral).

placodes as patches of about one hundred cells each, located within the ventral domain of parasegment 2. Invagination begins within the dorsal posterior corner of this placode (Fig. 1A and F, arrows), with cells that will form the secretory part of the tube invaginating first (green in Fig. 1E–H), followed by cells that will eventually form the Y-shaped duct connecting the two tubes to the larval mouth (Fig. 1B, magenta in E–H). The whole process, taking about 7 h in total, can be subdivided into roughly three stages that are likely guided by differing programmes of cell shape changes and rearrangements: (1) the early apical constriction and invagination, (2) continued invagination without active migration, (3) tube extension and positioning with active collective epithelial migration.

1.1. Early shape changes of salivary gland cells

1.1.1. Apical constriction and tissue bending

Once specified, the secretory cells within the salivary gland placode (Fig. 1E–H, green) elongate along their apico-basal axis with respect to the surrounding epithelium (visible in Fig. 1M) and position their nuclei basally (schematic in Fig. 2A; [4]). The increase in apicobasal length has also been observed in other tissues destined to undergo apical constriction and invagination, though the functional relevance is still unclear [5]. Only cells within the dorsal-posterior corner of the placode then begin to narrow their apical surfaces, initially without any active bending of the tissue (Fig. 1F,

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