Chapter 6. The directed self-assembly of bristles and hairs, surface contraction and mechanical coupling.

As apical surface contraction spreads across the wing blade, junctional complexes migrate to cellular vertices, with an ectopic microtubule organising centre (MTOC) near the distal vertex. Cytoskeletal components must continue to be delivered to the Ap cell surface as the hair shafts are extruded. A conical hair tip forms near the distal vertex with a basal pedicel that the migrates across the Ap surface towards a central location [1]. Both hair initiation and pedicel migration require cytoskeletal remodelling, regulated via Rho family GTPases (Rho, Rac and Cdc42), in addition to the core PCP gene functions [1 2 3 4]. The structural integrity of the Actin core of the hair shaft is dependent on the cross-linking proteins, ankyrin (Forked, F) and fascin (Singed, Sn), without which *f* and *sn* bristles and hairs become twisted and split. In general, PCP mutants develop multiple wing hairs [5], with imprecisely initiated foci [1]. The expression of motor-domain deleted MyoII may also induce multiple hair foci [6], consistent with imprecise hair initiation sites. During normal development, hair shaft migration may track the inward migration of cortical material from the cell boundaries. However, in *en-Gal4; UAS-pk*^{pk} wings, a central pedicel is formed, while the hair shaft appears to remain at the distal vertex (Fig. 8).

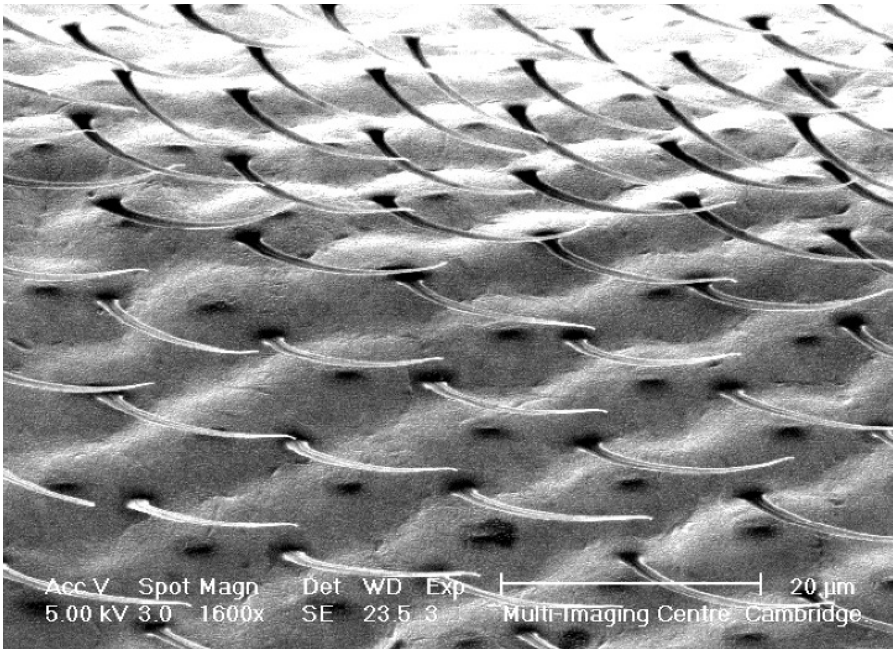

Fig. 8. Overexpressed Pk^{pk} displaces wing hairs. A central electron-dense spot marks the normal site of the pedicel, while the hair shaft remains near the distal cell vertex, SEM image. P compartment of *en-Gal4; UAS-pk*^{pk} wing blade. D. Gubb, unpublished.

By contrast, a hair shaft may be extruded directly from the centre of the Ap cell surface in *stan* mutants [7]. Strikingly, paired centrioles translocate to the distal vertex of wild-type wing cells before the hair shaft is initiated [8]. The simplest hypothesis may be that the hair pedicel is anchored to one of the two centrioles as it is translocated across the Ap cell surface.

In general, bristles are larger than hairs and they are formed from four cells in a sensory organ precursor (SOP). One of the four cells secretes the bristle shaft, while the other three provide neuronal innervation, insulation and a basal socket structure. As with hairs, the bristle tip forms a sharp conical point with an outer layer of actin fibrils and an inner

microtubule core. Bristle outgrowth may require dissolution of the extra-cellular matrix by the membrane-anchored Stubble (Sb) protease. Mutations within the extracellular stem of the Sb protease give short, malformed bristles with blunt tips [9]. During normal bristle development, the Sb protease is activated and released from its membrane-anchored stem, consistent with localised degradation of the extracellular matrix [10]. By implication, localised matrix dissolution may trigger remodelling of the underlying cytoskeleton. Meanwhile, the intracellular domain of Sb mediates transcriptional responses, via Rho, LIM kinase and the MyoII motor assembly [11]. The orientation of the bristle shaft is determined during the last cleavage division, consistent with terminal fate being allocated via asymmetric partitioning within the bristle SOP cluster, see below Chapters **22, 29**.

Summary:

Apical contraction of the wing disc epithelial cells generates a uniform hexagonal array, with AJs located preferentially to hexagonal vertices. Paired centrioles are anchored near the distal vertex, one of which migrates towards the cell centre together with the base of the hair. Hair translocation requires remodelling of the cortical cytoskeleton, together with fluid displacement of the plasma membrane. The precise initiation of a single hair near the distal cell vertex is disrupted in PCP mutants, with one, or more, hair pedicels migrating towards the cell centre. Microfilament bundles are stabilised by cross-links in the hair and bristle shafts, with an outer F-actin layer surrounding the inner microtubule core. The extracellular matrix may be locally degraded by the Sb protease during shaft extension, while the intracellular domain of Sb domain mediates transcriptional responses. Thus, the extrusion of hair and bristle shafts requires coordinated remodelling of the internal cytoskeleton and extracellular matrix.

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