simple approach gives a reasonable scaling for stratification in the Southern Ocean and the resulting strength of the Antarctic Circumpolar Current (in which it is generally thought that eddy fluxes are indeed a significant factor[9]). Moreover, predictions for other ocean basins give reasonable thermocline structures, hinting that this concept has much wider applicability than in just the Southern Ocean, and that a complete thermocline theory must consider the role of eddies.

It is early days for an idea that has not yet been adapted to realistic ocean conditions. But the first signs are encouraging: it may be large, horizontal eddies — rather than small, vertical ones — that control the ocean. ■

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Cell biology

A new view of photoreceptors

Franck Pichaud and Claude Desplan

The light-gathering structures in our eyes are specialized membranes found on cells known as photoreceptors. Two studies show that a protein called Crumbs is crucial for the development of these membranes.

The striking conservation of gene function from fruitflies to humans is under the spotlight again. On pages 143 and 178 of this issue, Pellikka and colleagues[1] and Izaddoost and co-workers[2] describe the role of the Crumbs protein in controlling the development of photoreceptors — the light-detecting cells in the eye — in fruitflies. The story is fascinating in itself, but also has implications for our understanding of the forms of two inherited human eye disorders, retinitis pigmentosa and Leber congenital amaurosis[3,4], in which CRB1, the human counterpart of Crumbs, is mutated. Indeed, much of what is already known about the CRB1 protein is based on its physical and functional similarity to the fruitfly Crumbs.

The study of developmental genes in fruitflies (*Drosophila melanogaster*) has provided deep insights into complex cellular processes that do not exist in simpler model systems such as yeast. One such process is that by which the 'top' and 'bottom' of an epithelial cell become distinct — a feature that ensures that epithelial tissues, such as those that cover the skin and line the gut, retain their highly polarized architecture. At the cellular level, this polarity relies on the vectorial segregation of different proteins to specific regions of the plasma membrane, thereby allowing a cell to distinguish top from bottom[5].

For instance, a complex consisting of the proteins Crumbs, Discs lost and Stardust, together with another complex involving Bazooka, specifies the apical membrane (that at the top) of *Drosophila* epithelial cells[6–9]. The basolateral membrane (that at the bottom) is characterized by a complex comprising Lethal giant larvae, Discs large and Scribble[10,11] (Fig. 1a). Two narrow circumferential membrane domains form at the boundary between apical and basolateral membranes; these domains are needed to allow neighbouring epithelial cells to interact. One of the domains, the zonula adherens, is enriched in the cadherin–catenin protein complex. The other, the marginal zone, is found just apical to the zonula adherens and is enriched in apical determinants such as Crumbs.

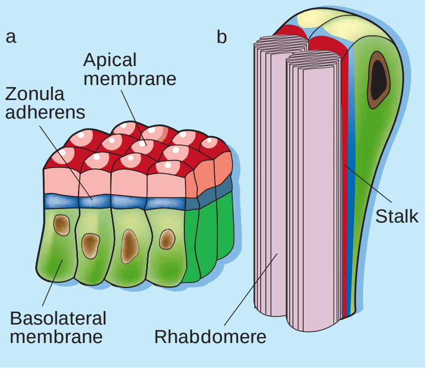

Figure 1 **Determinants of cellular polarity.** a, **Epithelial cells in the fly embryo. The apical part of the cell is in red, the zonula adherens is blue, and the basolateral part is green. The proteins Crumbs, Stardust, Discs lost, β_h-spectrin, Bazooka, protein kinase C and DPA-6 are present in the red areas; Armadillo/β-catenin, Canoe, Pyd and spectrins in the blue areas; and Lethal giant larvae, Discs large, Scribble and myosin II in the green areas.** b, **The same colour code is used for photoreceptors. The photoreceptor could be viewed as the equivalent of epithelial cells, but turned by 90°. The rhabdomere (light-gathering structure) is shown in purple; although the most apical membrane, it lacks Crumbs.**

Photoreceptors are a type of epithelial cell that undergoes a massive change in shape during development: their apical–basal axis rotates by 90° and the apical membranes elongate to form a long, densely packed array of light-sensitive membranes (Fig. 1b). These specialized membranes are called outer segments in vertebrates and rhabdomeres in flies. They originate from different apical extensions in vertebrates and invertebrates (from 'cilia' or 'microvilli', respectively[12]) and have different mechanisms for transducing light. Nevertheless, the final morphology is quite similar: both structures consist of packed apical membranes with high concentrations of a light-detecting pigment. The rhabdomere is supported by a specialized membrane, the stalk (Fig. 1b), which connects it to the zonula adherens; the vertebrate outer segment is similarly supported by the inner segment.

Knowing that Crumbs is involved in specifying apical membranes in *Drosophila* epithelial cells during development, Pellikka *et al.*[1] and Izaddoost *et al.*[2] wanted to find out whether this protein is also required for the massive changes that take place in the apical membranes of photoreceptors. Using the full range of tools available to *Drosophila* geneticists, including disrupting the function of the Crumbs gene in fly eyes, both groups discover a role for Crumbs in maintaining the integrity of the zonula adherens during photoreceptor development. In other epithelial cells, Crumbs is likewise involved in maintaining the zonula adherens, in order to specify the apical and basolateral membranes. But in photoreceptors this role is adapted to enable the rhabdomeres to elongate substantially. In addition, Pellikka *et al.* show that Crumbs has yet another function — to modulate the length of the stalk, recruiting new membrane as necessary to extend the stalk.

Interestingly, these two distinct processes — rhabdomere elongation and stalk extension — are mediated by two distinct regions within the Crumbs protein[1,2]. Crumbs is a transmembrane protein containing a sequence of amino acids known as a PDZ-binding motif (a protein-interaction motif) within its short intracellular region. The intracellular portion of Crumbs seems to be the only part needed for the integrity of the zonula adherens, and to specify apical membranes and facilitate rhabdomere elongation[1,2]. The very end of the intracellular domain recruits the Stardust protein, with the PDZ-binding motif recruiting Discs lost[6–8].

The extracellular part of Crumbs, on

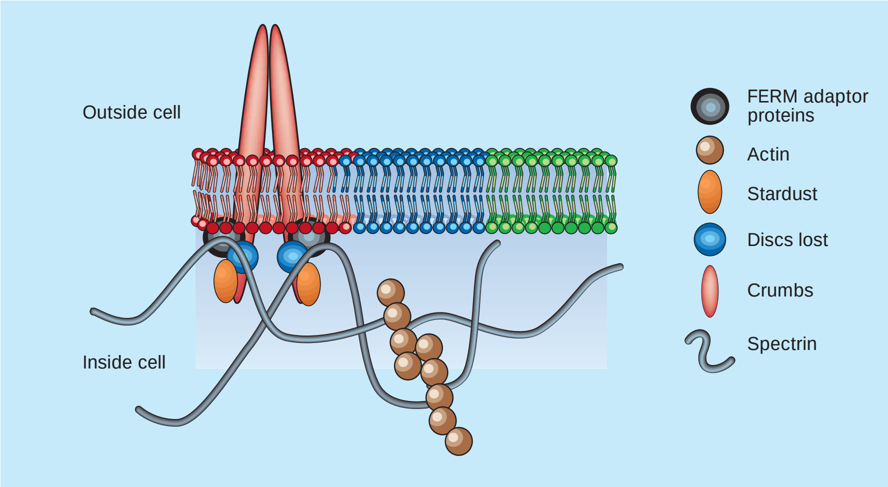

Figure 2 **How the unusual architecture of the photoreceptor apical membrane might develop (based on refs 1, 2). The photoreceptor plasma membrane is divided into stalk (red), zonula adherens (blue) and basolateral parts (dark green). Here, two Crumbs proteins interact through their extracellular domains. When the complex is attached to the membrane, the regions just inside the membrane can recruit FERM proteins and spectrin, anchoring the membrane to the actin cytoskeleton. This might lead to stalk elongation by decreasing the rate of membrane internalization. The intracellular regions of Crumbs also recruit the Stardust and Discs lost proteins; together, these three proteins contribute to the other function of Crumbs — specifying the apical membrane.**

the other hand, appears to be involved in modulating stalk length[1]. Pellikka *et al.* found that overproduction of a truncated version of Crumbs lacking the intracellular domain could increase stalk length in a dose-dependent manner. This is particularly exciting as the extracellular domain is not needed for Crumbs to determine apical–basal polarity.

How does Crumbs recruit extra membranes to lengthen the stalk? Although they were not looking at stalk formation, Izaddoost *et al.*[2] might have uncovered a mechanism. They studied a region of Crumbs known as the juxtamembrane domain, which is found just inside the cell[13]. Izaddoost *et al.* show that this domain is responsible for allocating material such as the cadherin–catenin complex to the photoreceptor's zonula adherens, independently of an effect on apical–basal polarity. They also suggest that the juxtamembrane domain could be a binding site for a certain 'adaptor' protein, which in turn would recruit components of the cellular skeleton such as spectrin. Interestingly, Pellikka *et al.* show that one form of spectrin does form a complex with Crumbs and Discs lost.

So we propose the following model. As mentioned above, Pellikka *et al.* found that overproduction of the membrane-bound extracellular region of Crumbs leads to stalk extension. We suggest that Crumbs interacts with itself through this extracellular region (Fig. 2). The complex produced could then signal through the juxtamembrane domain and recruit the spectrin cytoskeleton, which would in turn decrease the rate at which membrane is internalized in the cell and so favour stalk extension[14]. Consistent with this model, the stalk is shorter when one particular form of spectrin is mutated[1].

What light do these results[1,2] shed on the forms of the human disorders retinitis pigmentosa and Leber congenital amaurosis in which CRB1 is mutated? In vertebrate photoreceptors, CRB1 is localized to the inner segment[1], as is Crumbs to the stalk in *Drosophila*, pointing to these membranes as being functionally equivalent. So it will be interesting to see whether CRB1 defines the length of the inner segment in vertebrates, as Crumbs does in fruitflies. Moreover, some patients with retinitis pigmentosa type 12 have mutations that affect only the extracellular domain of CRB1, which is intriguing given that this portion of Crumbs is only crucial in stalk extension[1]. It seems that doctors are in a position to cast a fresh eye over these debilitating retinal diseases. ■

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Daedalus

Electric waves

Wave power is one of the renewable sources of energy that the British government wants to develop. Yet many gates and nodding ducks, which are used to capture energy from the surface waves, have been destroyed by a furious sea; only devices with no moving parts seem to have a future. Daedalus recalls that waves are not merely a surface effect. Much of their energy is stored deep under the water, in the form of circular or elliptical closed currents that reach right down to the sea bottom (which is why waves gain height in shallow water). And because sea water contains salt, it conducts electricity. So a fully submerged, static, electrical device should be a good bet.

Electrochemists hold that a piece of metal dropped in an electrolyte gives off positive ions. They dissolve; it takes up the opposite negative charge and attracts them. The result is a double layer, the negative metal sheathed in positive ions.

So, says Daedalus, imagine two pieces of metal held apart in the water by an insulator. Ions would be released from both sides. If the ions are pushed from one side to the other by a current in the water, the arrangement should gain energy. DREADCO engineers are now designing webs of such electrical conductors to be implanted on the sea bed, out beyond the low-tide mark. Much of the technology has already been perfected by gas-drillers and other marine engineers. Each unit will damp the wave over it and generate rather a lumpy alternating current. Rectifiers will turn this into direct current; all the units will be coupled in series. Statistically the final voltage should be fairly smooth, its intensity depending on the vigour of the incoming sea. It will be led ashore directly, through delivery leads.

To the waves above, this steady loss of energy will 'feel' like an energy-absorbing sea bed. A big distributed damping installation should steal so much energy from the seas that only safe little waves will hit the shore. If so, the new system will not only provide energy, but will also reduce the need for sea walls and other marine defences. Even the wildest sea will give safe, useful energy.

Considerable cunning will be needed to find the best layout for the system. Daedalus likes the idea of close pairs of conductors aligned to cut the most likely wave ellipses; but the final design must depend on empirical insights. Ships should also welcome the system — it will damp rough weather. Anchoring would not be advisable, however; it would damage the system.

David Jones