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VII. POLARIZED CELL DIFFERENTIATION

In symmetrically cleaving cells at their cytokinesis, a "contractile ring" is formed by the circumferential concentration of cortical actin and myosin-II filaments (Schroeder, 1972; Pollard *et al.*, 1990, see also IV.E.1.). By contrast, asymmetric, differentiating cleavage is mediated by a "contractile arc" which contains bundles of actin filaments of opposite polarities oriented parallely to the long axis of the cleavage-furrow (Mabuchi *et al.*, 1988).

Cytokinesis in diatoms involves a cleavage furrow rather than a cell plate and a band (preprophase) of microtubules coalesces circumferentially around the cell before the onset of mitosis (Wordeman and Cande, 1990).

Deviation from symmetric division occurs at female meiosis where the three unused chromosome complements are discarded in small cells called polar bodies. These bodies result from an unequal cell division generally attributed to the localization of the meiotic apparatus at the animal pole of the egg. Recently, however, polar body formation studied in the egg of the freshwater oligochaete *Tubifex attai* has been attributed to the reorganization of the cortical actin (Shimizu, 1990).

Embryonic mitosis also creates two different cell types which are placed in their appropriate position by the orientation of their division planes. For example, "in grasshopper embryos neuronal stem cells not only divide asymmetrically to give a nerve cell precursor (which is small) and a new stem cell (which is large), but also divide in a precise orientation so that the nerve cell precursor comes to lie internal to the more superficially located stem cell. Continued polarized divisions of the stem cell produce an ordered series of neuronal precursors, with the first born being the most internal. This polarity appears to influence the ordered structure of the nervous system since each neuronal precursor gives rise to different types of neuronal cells" (Doe and Goodman, 1985, O'Farrell *et al.*, 1989).

Factors inducing unequal cytokinesis have also been studied in grasshopper neuroblasts and found to be caused by the eccentric location of the spindle which maintains a definite polarity in dividing cells (Kawamura and Yamashiki, 1990).

A. Intercalary differentiations

1. *Bacterial endospores*

A novel mechanism of cell division has recently been described in a gram-negative bacterial rod by Mohn *et al.* (1990). Its polar growth occurs with a collar which girdles each cell.

3. *Fungal zoospores*

In the aquatic fungi Chytridiomycetes, the monoflagellate zoospores emerged from sporangia (see **I**, VII.B.1.a[2]) have an inherent structural polarity with regard to the apico-basal sequence: ribosomal nuclear cap - nucleus - nucleolus - rhizoplast - flagellum. The highly polarized zoospore of species of *Blastocladiella* shows a single, basally positioned mitochondrion (Cantino *et al.*, 1963) and that of species *Allomyces* a large kinetosome-associated basal mitochondrion sorted from the other ones (Fuller and Olson, 1971; Aliaga and Pommerville, 1990). In the other aquatic fungi Oomycetes, the zoospores of *Saprolegnia* are biflagellate and diplanetic, namely they sequentially change from the piriform to the reniform type. These last, symmetrical secondary zoospores display an asymmetrical arrangement of microtubules (Holloway and Heath, 1977): ''given the asymmetry of flagella themselves (whiplash versus Flimmer) some asymmetry in the microtubular root system might be anticipated''.

C. Apico-basal differentiations - heterobipolar axiation

1. *Caulobacterial cells (flagellate-stalk poles)*

Differentiation in Caulobacteria is high-lighted by an asymmetric cell division producing two different cell types, a motile swarmer cell and a slightly larger, nonmotile stalked cell (see **I**, Fig. 25); this cell cycle is subtly regulated (Newton and Ohta, 1990).

In a further study of the assembly of the two major polar organelles of *Caulobacter crescentus*, the flagellum and the stalk, Driks *et al.* (1990) have identified a polar particle (10-nm) as a new structural feature at the flagellate and the tip of the stalk. The characteristic asymmetry of the *Caulobacter* cell appears to be disrupted in mutants (*flbT*) in which the polar particle is absent at the flagellar pole.

4. *Cryptogamic spores (rhizoid-thallic poles)*

Signals controlling polar development of moss protonema and fern prothallia have been reviewed by Jaenicke (1991) who mentioned the fact that growing chloronemata of *Funaria hygrometrica* can be converted by indole acetic acid (IAA) into budding caulonemata by inducing an asymmetric division in this moss grown on agar at low light (Bhatla and Bopp, 1985).

5. *Higher plants cells*

b) *Epidermal cells*

Mechanoreceptor cells from the trigger hair of *Dionaea muscipula* Ellis are characterized by concentrically ordered cisternae of endoplasmic reticulum which occupy both basal and apical cell poles (Buchen *et al.*, 1983). To elucidate the

development of this polarity, electron microscopic examinations of these hairs were conducted at successive stages of differentiation (Casser *et al.*, 1985).

6. *Higher animal cells*

a^2 *Molluscs and Worms*

Embryonic development from the fertilized egg of the nematode *Caenorhabditis elegans* begins with series of *unequal* cell divisions that give rise to six founder cells (Wood, 1988; Riddle and Georgi, 1990).

a^3 *Insects*

Antimicrotubule chemicals such as colchicine or nocodazole disrupt cytoplasmic streaming within the late stages-oocyte of *Drosophila* and also lead to an abnormally positioned oocyte nucleus (Gutzeit, 1986a). Conversely, the antimicrofilaments cytochalasin B and D interfere with streaming from nurse cell to oocyte (Gutzeit, 1986b). Actin may thus be required for movement into the oocyte while microtubules may be necessary for proper placement within the oocyte.

a^5 *Amphibians*

The eggs of *Xenopus laevis* have been used as a model system to investigate the role of polarity in amphibian development. The presence of an animal/vegetal polarity within the *Xenopus* egg plasma membrane has been demonstrated with certain lipid probes which appear to partition into the plasma membrane and indicate the existence of lipidic microdomains when they recover upon photobleaching (Dictus *et al.*, 1984).

Xenopus oocytes have a high density of cholinergic (muscarinic) receptors clustered around the animal pole (Kusano *et al.*, 1982). Activation of these receptors generates inositol triphosphate (IP_3) which then releases calcium, which opens chloride channels (Oron *et al.*, 1985). The function of these calcium-activated chloride channels is unclear but, according to Berridge (1987), ''they could be responsible for the current that is known to enter the animal pole and that might be responsible for establishing the anterior-posterior axis that controls early development''. The same author has further suggested that, in the polar transduction of their message toward the cell center, IP_3 and diacylglycerol mediate the action of mitogenic factors e.g. fertilization and growth factors.

Following their experiements using anti-cytoskeletal agents, Yisraeli *et al.* (1989) proposed a model for the localization of Vg1 mRNA in which ''translocation of the message to the vegetal cortex is achieved via cytoplasmic microtubules and the anchoring of the message at the cortex involves cortical microfilaments''. Polarity of the surface and cortex of the amphibian egg has been studied from fertilization to first cleavage (Stewartsavage *et al.*, 1991).

b) *Epithelia (apical-basolateral poles)*

Epithelial cells display a structural and functional polarization implicating the division of their plasmalemma into apical and basolateral domains. The generation of this polarity has been unravelled by the discovery that animal enveloped viruses mature in a polarized fashion in infected epithelial cells, namely that, during infection a viral protein goes to the basolateral surface of the polarized cell (Rodriguez-Boulan and Sabatini, 1978 and ref. in **I**). Epithelial polarity in the presumptive myocardium can be demonstrated by polarized release of enveloped viruses in the embryonic chick heart (Peng *et al.*, 1990). Viruses have been shown to sort vectorially in either apical (influenza) or basolateral (vesicular stomatitis) membrane surfaces in monolayers of polarized kidney cells. There are stage-dependent differences in polarized budding of these two viruses.

Generation and maintenance of steep electrochemical gradients in transporting epithelia depend upon the compartmentalization of surface enzymes, ion, and metabolite transporting systems into the apical and basolateral domains of the plasma membrane (Rodriguez-Boulan, 1983). During biogenesis of epithelial cell polarity there occurs an intracellular sorting and vectorial exocytosis of an apical membrane glycoprotein (Misek *et al.*, 1984). Analogs of erythrocyte ankyrin have recently been found to be confined to the basolateral plasma membrane of transporting epithelia, neurons and photoreceptors (Drenckhahn and Bennett, 1987).

In the known asymmetric cell surface distribution of ionic pumps in epithelial cells (see **I**), the major driving force for the transepithelial transport of ions is the sodium pump. This Na^+, K^+-ATPase pump controls among many cellular functions, intracellular pH, free calcium concentration and membrane potential (Rossier *et al.*, 1987; see also IV.B.2d).

The meeting process in a cell-free assay that measures the fusion of apically and basolaterally derived endocytic vesicles with late endosomes requires the presence of polymerized microtubules, and also depends on the mechanochemical motors kinesin and cytoplasmic dynein (Bomsel *et al.*, 1990). Since microtubules in unpolarized cells radiate from the perinuclear region, where late endosomes are clustered, with their plus ends directed toward the cell periphery, Bomsel *et al.* (1990) suggest that "the centripetal movement of endosomes is expected to occur in a retrograde direction", involving a dynein-like activity (Vale, 1987 (**I**), see IV.E4).

The development of the polarized epithelial cell phenotype and the role of tight junctions in apical/basolateral membrane polarity has been reviewed by Rodriguez-Boulan and Nelson (1989), Cereijido *et al.* (1989) and Wandinger-Ness and Simons (1990). They all emphasize that the question of how epithelial cells generate and maintain this high degree of cell polarity remains still largely unknown. Recently, Watson *et al.* (1990) have used Na^+, K^+-ATPase as a marker to explore the factors governing apical/basolateral polarity during differentiation of mouse trophectoderm. They conclude that cell adhesion mediated by the protein uvomorulin (E-cadherin) is involved in spatially restricting the expression of the catalytic subunit of ATPase.

This subunit shifted from the basolateral to the apical plasma membrane when fully developed blastocysts were treated with cytochalasins. These findings of Watson *et al.* (1990) suggest "a primary role for the apical plasma membrane in the process of polarization, and implies that tight junctions are a manifestation of polarity that serve to maintain the separation between apical and basolateral markers".

Cadherin-bearing junctions (see IV.B.2b) are generally localized at the apical portions of cells (Rodriguez-Boulan and Nelson, 1989). The transfection of a fibroblast line with E (epithelial)-cadherin cDNA causes the polarized distribution of Na^+, K^+ adenosine triphosphatase, suggesting a function for the cadherin system in the establishment of cell polarity (McNeill *et al.*, 1990).

There is a lack of knowledge about spatial distribution of Ca^{2+} signal and of the Ca^{2+}-dependent ion channels in the secreting epithelial cells (Marty, 1987 in Kasai and Augustine, 1990). It has been found a polarization of $[Ca^{2+}]_i$ elevation and ion channel activation which suggested to Kasai and Augustine (1990) that this comprises a novel "push-pull" mechanism for unidirectional Cl^- secretion.

Dotti and Simons (1990) have suggested that neurons and epithelial cells sort viral glycoproteins in a similar manner. A recent report (Dotti *et al.*, 1991) of the polarized sorting of a glycolipid-anchored protein proposes that the mechanism of sorting of surface components may therefore be similar in neurons and epithelial cells. Both proteins and lipids must be segregated and transported differentially to the apical and basolateral surfaces. Lipids are known to be asymmetrically distributed among the various cellular organelles. Glycosphingolipids are preferentially enriched in the apical membrane. Glycosylation appears important for generating this polarized distribution. In the involvement of glycolipids in protein sorting, glycosyl-phosphatidyl-inositol acts as a "dominant" apical targeting signal (Lisanti and Rodriguez-Boulan, 1990).