MORPHOGENESIS OF DICTYOSTELIUM

Dictyostelium discoideum, a simple genetically tractable organism situated at the threshold of single and multicellular organisms in the evolutionary tree of life, is well suited for the study of these interactions because its genome has been sequenced and it is amenable to experimental manipulation through targeted gene disruption and replacement.

Dictyostelium cells normally live as single cells in the soil leaf litter where they feed on bacteria and divide by binary fission. Under starvation conditions up to several hundreds of thousands cells aggregate chemotactically to form a multicellular structure (the slug) that, directed by light and temperature gradients, migrates to the soil surface to form a fruiting body. The fruiting body is composed of a stalk supporting a mass of spores. The spores disperse and under suitable conditions germinate to release amoeba, closing the life cycle.

As Dictyostelium development occurs under starvation conditions, only limited cell divisions occur during multicellular development. Morphogenesis primarily results from the arrangement of differentiating cells in a regulative spatial pattern. Starvation induces changes in the gene-expression programme that result in the cells acquiring the ability to produce, secrete and degrade cAMP.

Through the expression of the cAMP receptor, the cells also acquire the ability to respond chemotactically to cAMP gradients. Unstimulated amoeboid cells are changing shape continuously by extension and retraction of pseudodpods in all directions resulting in a random walk.

In the presence of an external gradient of a chemoattractant such as cAMP, the cells persistently extend successive pseudopods in the direction of rising cAMP concentration while suppressing the extension of lateral pseudopods, which results in an efficient movement up the gradient.

Pseudopod extension is driven by actin polymerisation, which provides the driving force for extension and simultaneous disassembly of the myosin thick filaments in the cortex at the site of extension as well as localised delivery of membrane and or proteins to allow extension to occur. Cells also need to pull up their back end and suppress the extension of lateral pseudopods. To move forward the cells must gain traction from the substrate on which they are moving. It appears that cells may undergo alternating phases of actin-driven extension at the front and myosin-driven contraction at the back.

Aggregation is caused by periodic cAMP synthesis and secretion by cells in an aggregation centre. Detection and amplification of this signal by surrounding cells coupled with desensitisation of the cAMP-producing cells results in the propagation of waves of cAMP from the aggregation centre outward. These waves of cAMP guide the chemotactically moving cells towards the aggregation centre, where they accumulate into a threedimensional aggregate: the mound. Initially, the cells move towards the aggregation centre as individuals, but after 10–20 waves have passed they form bifurcating aggregation streams, in which the cells make head-to-tail contacts via calcium-independent adhesion molecules, contact site.

Mound and slug formation

After the cells have aggregated, they form the hemispherical mound. Mounds are characterized by rotating waves of cAMP that direct the counter-rotational periodic movement of the cells. Cells start to differentiate into prespore and prestalk cells during aggregation, on the basis of physiological biases like nutritional state and cellcycle position at the time of starvation already present in the population before aggregation. Some prestalk cells then sort out to form the tip and the slug tip guides the movement of all other cells thus acting as an organizer. The tip's action as an organizer can be mimicked by the periodic injection of cAMP pulses of the right frequency and duration. Cells in the tip often rotate perpendicularly to the direction of slug migration, especially when it is lifted from the substrate. In the posterior part of the slug, the cells move forward periodically and all cells move on average with the speed of the whole slug.

Differentiation

A major goal is to understand the relationship between cell movement and the signals that control differentiation. These signals must be able to maintain the correct proportion of the prespore and prestalk cell types in an environment of extensive cell movement and changes in shape of the slug. cAMP pulses control the expression of aggregation-stage genes necessary for cAMP relay and cell–cell contact and can control prespore cell specific gene expression in later development. Prespore cells, in turn, produce DIF, which controls the differentiation of pstO cells. DIF spreads by simple diffusion from the prespore zone in adjacent regions where it controls the differentiation of prestalk O cells and possibly rear guard cells.

The switch from migrating slugs to fruiting body formation (culmination) appears to be controlled by a fall in ammonia concentration.

Multicellular Dictyostelium morphogenesis results from the chemotactic movement of thousands of differentiating cells coordinated by propagating waves of the chemoattractant cAMP produced by these cells. The dynamical interactions between the cAMP waves and the resulting chemotactic movement of the cells is formally sufficient to explain aggregation, stream and mound formation. Slug formation and culmination require the emergence of prespore and several prestalk cell types that show distinct cAMP signalling and movement properties. Only prestalk and anterior-like cells relay the cAMP signals while both prestalk and prespore cells move chemotactically in response to these signals.

MORPHOGENESIS OF ACETABULARIA

Acetabularia is a green, unicellular alga. The cell is giant reaching 3-5 cm in length at the end of vegetative growth, and contains a single nucleus, located in the rhizoid. It is remarkable, in that the alga withstands enucleation. Anucleate algae not only survive up to 40 d and carry on photosynthesis and other physiological activities, but also perform cap morphogenesis. The young alga germinates from a microscopic zygote giving rise to a small stalk directed upwards, and to protuberances at the opposite end that will differentiate into the rhizoidal outgrowths which fix Acetabularia to the anfractuosities of rock.

From the very beginning of growth, the cell is polarized. Early in its development, a hair whorl is formed at the subapical part of the stalk. The nucleus is located in the thick rhizoid, which grows little compared with the stalk. Successive hair whorls are formed, the older ones falling off. 'Three to six such 'coronae' are thus seen simultaneously on an alga 3-5 cm long. On the apex is another series of hairs, just differentiated, which are directed upwards. The number of hair whorls and the length of the stalk are related not only to the developmental stage, but also to external conditions. The hair's cytoplasm is not separated from the rest of the cells: there is a wall constriction, and through this the cytoplasm is continuous throughout hairs, stalk and the outgrowths of the rhizoid; so is the huge vacuole.

The final stage is the development of a species specific cap. The above-described process takes 1-3 yr in natural conditions. When cap formation is complete, the nucleus in the rhizoid enters meiosis, which is immediately followed by a wave of mitoses, resulting in a huge number of secondary nuclei. They migrate from the rhizoid to the stalk and finally to the rays of the cap. If the cap is torn away, cytoplasmic signals provoke dramatic changes in both ultrastructure and physiology of the nucleus.

Under favourable conditions, the cap is formed. The secondary nuclei invade the cap rays, accompanied by chloroplasts and mitochondria. The cytoplasm of each ray divides as walls form to produce about 80 cysts per ray, each containing one secondary nucleus, chloroplasts and mitochondria. Each cyst nucleus divides in turn several times. As a result of another differentiation, each cyst forms numerous gametes. In spring, the cap disintegrates. The cysts germinate: a small valve opens up and biflagellate, positively phototactic gametes are released. Liberated in sea-water, the gametes copulate and give rise to zygotes.

GROWTH AND CAP MORPHOGENESIS:

The most extensively studied aspects of development are stalk growth and cap differentiation. The early grafting experiments of Hammerling and co-workers in the 1930s demonstrated that the Acetabularia species specific cap morphology depends on its specific nucleus (Hammerling, 1953). The nucleus synthesized ' morphogenetic substances' which accumulated at the apex and controlled the specificity. Brachet demonstrated that the 'morphogenetic substances' were ribonucleic acids. The nucleus contains all the information for the morphogenetic traits. The mRNAs are, however, masked in some way until the appropriate time, and are ultimately expressed in succession during development, conditions permitting.

Acetabularia displays a highly polarized morphology, with an apex, a median region and a rhizoid. The mRNAs accumulate at the apex, as do some organelles. Almost every molecule playing a role in development is distributed according to an apico-basal gradient. The gradient can be positive (greater concentration of a particular molecule at the apex of the cell) or negative (the converse).

GRAFTING EXPERIMENTS OF HAMMERLING

He took two species *A. mediterranea* with a characteristic of 81 rays and rounded tips and *A. crenulata* with a cap of 31 rays and pointed tips. The algae are capable of regeneration from any part. So that cap, stalk or even nucleated rhizoid portion is removed, it will soon regenerate and give rise to a whole plant. But the enucleated portion on continuous decapitations (or removal) loses the regeneration capacity whereas the nucleated region always retains the regeneration capacity.

He grafted the stalk of *A. crenulata* with the rhizoid region *A. mediterranea* Vibecity

Then he grafted the rhizoid region of both the species (2 nuclei from both species in a common cytoplasm). Upon regeneration, all were of an intermediate type cap.

Further removed the stalk and allowed to regenerate. Upon regeneration the second cap formed was similar to that of cap of species that provides the nucleus.

An intermediate cap is the result from the rhizoid with nucleus of both the species (two nucleus in a common cytoplasm). The result clearly proved beyond doubt that nucleus is the site of hereditary material and not the cytoplasm.

The type of the cap is determined by the nucleus present in the rhizoids.

If both the nuclei are present in the same cytoplasm, an intermediate type of cap develops.

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