

Moonlighting organelles—signals and cellular architecture

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How living beings acquire novel functions has remained one of the most difficult questions of evolutionary biology, because to confer a selective advantage, a structure has to be functional. It is not sufficient that a precursor structure anticipates its future job; it must actually work during each point of the evolutionary transition. How can this be achieved under the constraint of continuous small changes and a progressive loss of the original functionality? A way out of the dilemma is so called preadaptation, where a structure conveys more than one function. In addition to its evident job, it can carry a second, often hidden or implicit, function that, upon changing conditions, can become central. The developmental and evolutionary flexibility caused by these “moonlighting” functions (Kurakin 2005) might be central not only for the self organisation of cells and organisms, but as well for macroevolution of new body plans. Common cellular manifestations of moonlighting are structures that at first sight are part of cellular architecture but simultaneously participate in signalling. Four contributions to the current issue illustrate the case:

Plant cytoskeleton: architectural lattice and sensory platform

Half a century has passed since microtubules were discovered by Ledbetter and Porter in plant cells after being predicted by Paul Green based on biophysical considerations. Their guiding role in cellulose synthesis and thus in the control of cell axis and morphology has turned into textbook knowledge. However, the details of this interaction are still on the move. Since plant cells have to adapt their

morphogenesis with the requirements of their environment, the interaction between microtubules and cell wall must be target of signalling. Phospholipase D as linker between microtubules and plasma membrane seems to be a central player in this context. In the “New Ideas in Cell Biology” of the current issue, Gardiner and Marc (2013) propose that phospholipases D, A2 and C are central for the communication between microtubules and cellulose microfibrils. This communication might imply microtubule-linked phospholipase activity organising the crystallisation of cellulose, but also, in reverse direction, the control of membrane fluidity constraining the movement of cellulose synthase complexes. Already 5 years ago, a second mechanism (independent of the direct linkage between microtubules and cellulose synthases) had been proposed for the orientation of cellulose (Pickard 2008) and structurally linked with the “plasmalemmal reticulum”, a netlike proteinaceous substructure at the plasma membrane. Are phospholipases integrated into this network?

Not only microtubules but also actin filaments can, in addition to their architectural role, mediate signalling. The work by Xu et al. (2013) was motivated to understand the cellular mechanism of cold-triggered male sterility in the wheat line BS366, a valuable tool for hybrid breeding. From a comparative transcriptome analysis, they identified actin as central factor. Since the role of actin in meiosis is far from understood, they investigated the role of actin in male meiosis. They describe that actin filaments are found in the meiotic spindle, a phenomenon that is unusual for mitotic divisions and only described for the *brick1* mutant of maize (Panteris et al. 2009). They further discovered a lantern-shaped actin structure that seemed to be linked with the phragmoplast. In fact, this actin lantern became disorganised upon cold treatment which was followed by a failure in the organisation of the cell plate. A specific subpopulation of plant actin subtending the membrane controls membrane stability and fluidity (Hohenberger et al. 2011). The findings by Xu et al. (2013) indicate that, in reverse direction, actin

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can perceive and transduce changes in membrane fluidity into responses of subcellular organisation.

Centrioles: microtubule anchor and cellular memory

Centrioles are the major organiser for microtubules in many eukaryotic cells. Their evolutionary origin is closely linked with the basal body of eukaryotic flagella, illustrated by the loss of centrioles in seed plants where flagellate spermatozoids have been replaced by a pollen tube. When Haeckel is right and ontogeny recapitulates phylogeny, it should be possible to see the transition from centrioles into flagellar basal bodies during individual development. Model systems to study this developmental transition have been the gametangia of the brown alga *Ectocarpus siliculosus*. Motomura et al. (2013) follow flagellar development by high-performance TEM and electron tomography. They can visualise with high spatial and temporal resolution, how centrioles differentiate into basal bodies and attach with their distal basal plates to the plasma membrane. At the attachment site, the membrane forms a concave pocket into which vesicles and cytoplasm accumulate to drive the elongating flagella.

Again, this architectural role of an organelle can be accompanied by a second function that is less specific and related to signalling. In our “New Ideas in Cell Biology” section of the current issue, Chichinadze (2013) reviews the spectacular finding that centrosomes contain specific RNA termed cnRNA. The search for nucleic acids in the centrosomes was motivated by the fact that the other three self-replicating organelles (nucleus, mitochondria and plastids) all contain DNA, and Margulis’ theory that centrosomes also derive from an endosymbiotic (probably *Spirochete* like) ancestor. The discovery of cnRNA was originally discussed as specific subcase of the general affinity of nucleic acids for microtubules, which is the base of a large number of mRNA transport phenomena during embryogenesis, for instance during the polarisation of the fruit fly zygote. A closer look on the identity of these cnRNA revealed,

however, both specificity of these RNA species as well as novel functions (that are still under debate). The author links these findings to evidence for the role of centrosomes in cellular ageing, i.e. centrosomes (by virtue of the cnRNA stored in their interior) would provide something like a cellular clock that advances each time, when a cell divides resulting in a limited life span ensuring a kind of inbuilt “quality control” for division. Thus, centrioles would act as a kind of “cellular memory” storing and transmitting information—again a moonlighting function that occurs in the shadow of the explicit structural role they play for the organisation of microtubules (a function that, by the way, can be conveyed in many cell types by other “moonlighters” such as the nuclear envelope of higher plants).

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