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EDITORIAL

The *Oberhäutchen* principle—growth and integrity

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Growth as central task for life is, at the same time, a challenge for integrity: A growing cell has to continuously increase its surface and the same holds true for a growing organism. At the same time, the integrity of the surface must never be interrupted at any single time point to prevent the chemical gradients sustaining life from breaking down immediately. There is only one possible way to resolve this dilemma: the new surface has to be *prepared* before it will be exposed as novel outer interface. This seemingly trivial strategy is far from trivial in its realisation, because it requires a high level of synchrony and integration. Two contributions in the current issue, from quite different models, show in interesting structural and spatial detail how novel surfaces are generated during growth and division.

Life conquered solid land by generating water-impermeable surfaces. The cuticle of vascular plants or the keratinised skin of land vertebrates fulfils the same function: to reduce water loss by transpiration. The importance of this skin is illustrated by the fact that the amphibians with their single cornified layer are confined to humid habitats, whereas the thick, horny scales of reptiles allowed these animals to expand into arid, otherwise inaccessible, habitats. The skin of lizards and snakes is composed of several cell layers subtending a single layer of cornified cells, the protective *Oberhäutchen*. This protective skin has a price: due to its fibrous composition it is not very extensible and therefore impairs growth. To increase in size, snakes must therefore shed their skin including even their cornea. This event is orchestrated with high synchrony and requires that the surface is completely renewed whilst the protection granted by this surface has to be perpetuated. The work by Alibardi (2014) in the current issue describes how these antagonistic requirements are reconciled in the model *Pantherophis guttatus*. Before the moult is discarded, a specific shedding complex will form, along which cell junctions are degraded. This shedding complex is subtended by the prospective *Oberhäutchen* of the next generation. The preparation of the novel surface within the epidermis is accompanied by strong fluctuations of so-called beta keratins. These proteins were originally thought to be keratins similar to the structure-giving alpha-keratins of reptile scales, but later found to be non-homologous proteins that are complexed with alpha-keratins during cornification. Molecular information available for this model snake has now allowed identifying a specific protein from this group, which is rich in glycine-cysteine and associated with the shedding complex and allows for moulting, whereas the same protein disappears in the deeper so-called mesos-region and thus enables the formation of a new solid skin of the next generation. The (rich) abundance of transcripts for this protein does not match the relatively scarce incidence of the respective epitope as detected by immunofluorescence indicating a considerable degree of post-translational regulation. This functional repartitioning might be one of the mechanisms that synchronises the shedding of the old skin with the maturation of the new surface.

The snake *Oberhäutchen* is thus safeguarding integrity whilst enabling growth. The same problem has to be solved by individual cells during division. In their study on cell division, Nagasato et al. (2014) analyse cell division in the model brown alga *Silvetia babingtonii* in all its three-dimensionality making use of electron tomography. The problem to safeguard integrity whilst separating two daughter cells has been solved by different strategies in the different eukaryotic lineages: the cells of animals use a contractile actomyosin ring to furrow the daughter cells and a microtubular midbody to organise the final cut (Byers and Abramson 1968). Land plants employ a strikingly different mechanism: in the central

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cytoplasm between the daughter nuclei, a disc-like structure is generated that subsequently extends centrifugally by fusion of Golgi-derived vesicles till the daughters are separated (Hepler 1982). Again, this separative structure is organised and guided by a specific microtubular structure, the phragmoplast. Brown algae have evolved multicellularity independently from land plants and therefore provide an interesting case. Interestingly, both mechanisms can be found in this group—whereas in Fucoid algae cleavage proceeds in centripetal direction, driven by a central actin plate (Bisgrove and Kropf 2004), other lineages of the brown algae use centrifugal cleavage, similar to land plants (Nagasato and Motomura 2002), raising the question, how the new membrane can be prepared and kept in place over a considerable area to prevent membrane leakage during delineation of the daughter cells. The authors used sophisticated rapid freezing and freeze substitution in combination with electron tomography to get insight into the spatial organisation of membranes during zygote cytokinesis. They report amorphous membrane structures near the endoplasmic reticulum between the daughter nuclei that become aligned with the plane of division. This structure is composed of flat cisternae that now generate recruit vesicles at their periphery to produce a membranous network, which will fuse into a membranous sac that consists of flat and swollen domains. The swollen parts are covered with coated pits that are subsequently flattened by endocytosis of excess membrane material. Such structures form at different domains of the separation plane and progressively interconnect through the expanding membranous networks around them. With progressive maturation, the thickness of the membranous sac is homogenised until a continuous separation layer is achieved that now reach the pre-existing cell membrane at the prospective junction of cross wall and pre-existing cell membranes. The detailed insight into the details of separation made possible by cutting edge electron microscopical methodology reveals an astounding degree of spatial synchrony leading to the question, how obviously local processes can be integrated into a concerted activity reaching over the entire cross-section of the dividing zygote.

Although the molecular and cellular players as well as the system levels are of course different between the *Oberhäutchen* of a moulting snake, and the new cell membrane of a dividing plant cell, both processes solve, obviously very successfully, the problem of spatial integration and share (at least) one commonality: repartitioning as correcting mechanism. In case of the *Oberhäutchen*, it is the repartitioning of the glycine-cysteine rich beta-protein epitope, in case of the brown algal division, it is endocytotic recycling of excess membrane material in the swollen membrane sac that are used to cross-correlate different regions of the emerging new interface. Thus, the principles of self-organisation might be more similar than the molecules used for their realisation.

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