EDITORIAL

Negotiating on identity—glimpses on biological borders

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All organisms need a border delineating an internal space that is buffered against the fluctuating challenges of the outer world. These borders, at the same time, have to reconcile stability with dynamics and therefore are anything else but simple surfaces. Evolutionary processes very often are targeted to changes of biological borders, for instance, when organisms intrude (or are devoured) and subsequently maintain a partial border integrity. It is mostly the extent to which this border integrity is maintained or modulated that sets the frame for interactions that can range from symbiogenesis to biotrophic pathogenicity. The selective permeability of borders will ensure the maintenance of an internal homeostasis, and specific adherence to cell borders often defines the specificity of organismal interactions. In other words, biological borders are the sites where the identity of organisms is negotiated by interaction with the external world including other organisms. Several reviews and original papers in the current issue highlight different aspects of this fascinating biological phenomenon for examples from different domains of life.

Microtubule-based flagellar beat represents, along with amoeboid movements, a central mechanism for eukaryotic motility and is located at the external border of many protozoan, animal, and generative plant cells. The evolutionary origin of eukaryotic flagellae seems to be linked with originally ectoparasitic spirochaete-like bacteria that subsequently were domesticated in consequence of an endosymbiotic event. This might be one explanation for the fact that flagellae, in many aspects, behave as closed regulatory systems posing

interesting questions with respect to the maintenance of their homeostasis. The work by Williamson et al. (2012) in the current issue investigates how the transport of flagellar components to the growing tip of the flagellum is balanced with the exit of turnover products. This transport involves directional microtubule motors (kinesin-II for transport to the tip and dyneins for the retrograde transport) that form two complexes, termed A and B. Using conditional temperature-sensitive mutants of the model *Chlamydomonas reinhardtii*, they can show that the B complex confers dynein import, whereas the A complex is responsible for dynein exit from the flagellum. The initiation of flagellar differentiation is linked with a widely distributed, functionally diverse group of proteins, called centrins, reviewed by Zhang and He (2012) in the current issue. These calcium-binding proteins are organised in distinct domains that differ in structure and confer quite diverse functions to the different members of the centrin family. In addition to a participation of microtubule nucleation, they have also been shown a long time ago to participate in flagellar function (Melkonian 1979). These centrin functions are surprisingly divergent and can be not only structural, as shown for one of the *Chlamydomonas* centrins associated with the inner dynein arms, but also regulatory, as centrin 1 from *Paramecium caudatum* that controls the calcium channels that are responsible in ciliary reversal.

Although the border usually is located at the outer surface of an organism, this does not necessarily need to be the case. The endodermis of vascular plants represents an interesting exception of the rule that the border is outside. Whereas the outer layers of the root allow free diffusion of the external medium by mobility through the apoplast, the endodermis sorts and selects nutrients and ions and thus represents the true border, where a fluctuating exterior is separated from a buffered interior. The core element of this border function is a cell-wall modification, where a water-impermeable

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suberin layer blocks apoplastic flow forcing the medium through the filter of the plasma membrane. The anatomical features of this Casparian strip had been studied in great detail since its discovery in 1865, and the commitment for an endodermal cell fate by diffusible transcription factors could be elucidated a decade ago. However, it has remained obscure until recently, how the equatorial domains of the endodermal cell are committed for transport of the suberin ring. The review by Alassimone et al. (2012) in the current issue surveys the discovery of the novel CASP proteins that represent key components of this polarisation process and seem to guide the localisation of specific transporters to the central or distal faces of the endodermal plasma membrane showing interesting mechanistic analogies of this "inner skin of plants" with polarised epithelia characteristic for animals. However, partitioning of apoplastic and symplastic transport by Casparian strip-like structures seems to exist also outside the root, although the endodermis represents the best known example. In gymnosperm leaves, similar structures seem to control symplastic transport and phloem loading (Liesche et al. 2011).

The complexity of biological borders is illustrated by a third model, reviewed by Bak et al. (2012) in the current issue. They consider cases of viral transmission, where the virus does not undergo a specific propagation cycle in the vector organism, but is just attached to the exterior. For instance, the cauliflower mosaic virus binds to specific structures of the exterior mouthparts of the transmitting aphid and thus can cross the plant boundary during the feeding process. This seemingly trivial mechanism reveals upon closer scrutiny a surprising degree of complexity, where the viral particle forms a transmission complex with specific helper proteins that mediate the binding to a specific protein receptor in the specific acrostyle domains of the aphid stylet. Upon entering the host cell, viral particles enter the nucleus and are decapsidated and propagated. They subsequently reprogramme the host cell to emit specific volatiles and initiate chlorosis, both signals that will attract further aphids to close the life cycle.

References

Alassimone J, Roppolo D, Geldner N, Vermeer JEM (2012) The endodermis—development and differentiation of the plants inner skin. Protoplasma. doi:10.1007/s00709-011-0302-5

Bak A, Irons SL, Martinière A, Blanc S, Drucker M (2012) Host cell processes to accomplish mechanical and non-circulative virus transmission. Protoplasma. doi:10.1007/s00709-011-0328-8

Liesche J, Martens HJ, Schulz A (2011) Symplasmic transport and phloem loading in gymnosperm leaves. Protoplasma 248:181–190

Melkonian M (1979) Ultrastructural-study of the flagellate *Tetraselmis cordiformis* Stein (Chlorophyceae) with emphasis on the flagellar apparatus. Protoplasma 98:139–151

Williamson SM, Silva DA, Richey E, Qin H (2012) Probing the role of IFT particle complex A and B in flagellar entry and exit of IFT-dynein in Chlamydomonas. Protoplasma. doi:10.1007/s00709-011-0311-4

Zhang Y, He C (2012) Centrins in unicellular organisms: functional diversity and specialization. Protoplasma. doi:10.1007/s00709-011-0305-2