A cell biologist on Mars—the exotic world of algal cells

Peter Nick

© Springer-Verlag Wien 2013

In his famous book “An anthropologist on Mars,” Oliver Sacks presents exotic cases of neural disorders, and while describing the seemingly extraterrestrial world of these patients, he unveils the hidden wonders in the brain of the “normal” majority. In the history of science, very often, the fascination for the abnormal, exotic and mysterious has paved the way for a deeper understanding of the apparently “conventional.” Cell biology is no exception to this rule. It seems that the era of channelling towards a few model systems accessible for molecular approaches is now progressively replaced by a wider approach towards the variations of life. The renewed interest for “off-track” models is certainly fuelled by the advances in sequencing technologies that allow molecular insights even for models carried by only smaller research communities. Why are these “off-track” models important for science? New complex traits, such as new morphogenetical programmes, physiological achievements or metabolic pathways seem to emerge mainly from functional shifts of the underlying cellular and molecular events. These shifts would not be possible in systems where a function is exactly fitted to its current function. However, to quote a famous metaphor by François Jacob (1977), evolution is tinkering (and therefore neither design nor intelligent...), which means that most proteins are not exactly fitted, but in addition to their main function, maintain the ability for other hidden functions. In a different functional context, these moonlighting functions (Kurakin 2005) can take the lead. The heterogenous group of “algae” comprising highly diverse life forms with a mostly phototropic lifestyle provides good examples to illustrate the case, and the study of these seemingly extraterrestrial models might help us to get track of one or the other “moonlighting function” hidden in the cell biology of “higher” life forms. The current issue assembles several fine examples of algal cell biology:

The tinkering approach of evolution is neatly illustrated by the generation of new life forms through endocytosis. The review by Stork et al. (2013) in the current issue gives a survey on the

current state of the highly dynamic and highly controversial field of secondary endosymbiosis with green or red algae (that unlike stated in the last editorial to the current state of knowledge arise from primary endosymbiosis, as noticed by attentive readers). Secondary endosymbiosis gave birth to many important groups of “algae” including heterokontophytes (for recent review, see Beakes et al. 2011), haptophytes, cryptophytes, and flagellate parasites. A core element for the functional integration of formerly independent organisms into a novel supraorganism is the protein transport across the membranes between the symbiotic partners. Especially the transport across the second outermost plastid membrane that is derived from the former endosymbiont represents a major challenge. The review shows how the ER-dependent degradation machinery of the endosymbiont was remodelled and relocated to generate a novel transport machinery carrying the new task of importing proteins across the former cell membrane. Thus, evolution is not only “tinkering” by recycling pre-existing machineries into a new functional context, evolution apparently is also playing with modular “LEGO” bricks of function. The challenge will be to understand how tinkering is reflected in the networks of gene regulation.

One of the most mysterious and fascinating groups of “algae” are the diatoms that are treated by even two research publications in the current issue. Already by their lifestyle as pure diatoms, they appear a bit alien within the plant kingdom and their mysterious mode of locomotion, as well as their beautiful silica shells (that have inspired art and architecture alike) support the impression of a highly exotic form of life. Although minute in size, diatoms are of global impact and account for an estimated one fourth of the global cycles for silicium and carbon. Despite this impact, the question, how the unique, filigrane and species-specific silica patterns (the so called *frustulae*) are actually formed, has remained enigmatic. It was in this journal, where for the first time the electron microscopical detection of minute particles in the cytoplasm of diatoms was reported and these particles were proposed to represent transport vesicles for silicon (Schmid and Schulz 1979). This observation is now revisited by the work of Annenkov et al. (2013) in the current issue, but using a fluorescent dye specific for growing siliceous *frustulae* such that the function of these vesicles could be addressed by life-cell

P. Nick (✉)
Karlsruhe, Germany
e-mail: peter.nick@kit.edu

imaging. They used silicon starvation to achieve a synchronisation of silicon deposition—a simple, but smart approach from classical physiology to resolve the temporal sequence of causal chains. They can show that within minutes after readdition of silicon together with the specific dye, fluorescent vesicles appear in the cytoplasm and subsequently disappear again while siliceous valves are deposited. This study not only supports the classical hypothesis by Schmid and Schulz (1979) that the cytoplasmic particles are silicon transport vesicles but also resolves a two-stage mechanism of rapid Si uptake followed by a slower deposition of silicon into the growing *frustulae*. A second mystery of diatoms, their enigmatic mode of locomotion, is addressed by the work of Wang et al. (2013) in the current issue. Again, the starting point was an observation published in this journal (Edgar 1983): diatoms moving over benthic surfaces secrete considerable volumes of mucilage, and the so called Edgar model assumed that motility is generated by a conformational change of the adhesive mucilage during its secretion. The direction of secretion was thought to be confined by actin to one end of the cell such that it is pushed forward. This model, although appearing plausible, suffers from several weak points that stimulated the authors to search for a better model. For instance, it is not clear how sign reversals of movement might be generated by the Edgar mechanism. The authors analysed cell structure, movement, mucilage and bending deformation for the benthic pennate diatom *Navicula* and come up with a new model, which is also supported by biophysical modelling, where pseudopodia protrude from the *frustulae* attach to the surface through secreted extracellular polymers and where other pseudopodia push against the substrate providing the driving force for locomotion.

Brown algae harbour the most differentiated life forms among the algae and can produce highly sophisticated architectures. Due to this complexity, these architectures have to be tuned with respect to their environment mainly with the distribution of light in their benthic habitat. Therefore, the zygotes and spores of brown algae are photosensitive and adjust axis and polarity with the direction of light during a photosensitive period. The photopolarisation of the *Fucus* zygote has been extensively studied in the second half of the last century and led to a model, where light-triggered calcium currents drive a transcellular gradient of actin-dependent calcium channels such that initial weak gradients are self-amplified into a robust polarity by a process that had been termed “self-electrophoresis.” A drawback of *Fucus* system has been the lack of molecular information and during the abovementioned channelling upon few models; this beautiful system for cellular development has been mostly abandoned. It seems that the new move towards genomics of “off-track” models will also bring a renaissance of brown algae as systems for plant development. The related species *Ectocarpus siliculosus* has been sequenced and is currently pushed as new genetic model. Here, the mitospores can be polarised by light in a manner that resembles the situation in the *Fucus* zygote. The work by Green et al. (2013) in the current issue investigates the

role of microtubules in polarisation. They show that pharmacological manipulation of microtubules impairs polarisation, an even stronger inhibition can be produced by inhibitors of vesicle flow. By confocal microscopy, they visualise a radial array of microtubules emanating from an organelle that resembles a centrosome and is localised close to the nuclear rim. Upon germination, this array gives rise to longitudinal microtubules that reach into the bulging filament. Within the filament, mitotic spindles are aligned with the axis of growth. The characterisation of these cellular events is important as phenomenological framework to interpret phenotypes for future studies on the functional genetics of polarity induction. *Ectocarpus* differs in a curious detail from the classical *Fucus* system: polarity induction in *Fucus* is a matter of actin and microtubules seem to be dispensable in this context. In the *Ectocarpus* system, it is microtubules that take the lead—the authors suggest that this difference might be linked with the presence of a centrosome in case of the *Ectocarpus* mitospores, whereas in *Fucus*, the centrosomes are paternally inherited (Motomura 1994). This detail shows that even in cell biology, often perceived as science searching for general laws, details and particularities of models are relevant and can when they are seriously considered by comparison allow for new mechanistic insights (a topic addressed in a previous editorial, Nick 2009).

Conflict of interest The author declares that there is no conflict of interest.

References

- Annenkov V, Basharina TN, Danilovtseva EN, Grachev MA (2013) Putative silicon transport vesicles in the cytoplasm of the diatom *Synedra acus* during surge uptake of silicon. *Protoplasma*, current issue
- Beakes GW, Glockling SL, Sekimoto S (2011) The evolutionary phylogeny of the oomycete “fungi”. *Protoplasma* 249:3–19
- Edgar L (1983) Mucilage secretions of moving diatoms. *Protoplasma* 118:44–48
- Green JJ, Cordero DF, Peters NT, Logan KO, Kropf DL (2013) Dynamic Microtubules and Endomembrane Cycling Contribute to Polarity Establishment and Early Development of *Ectocarpus* Mitospores. *Protoplasma*, current issue
- Jacob F (1977) Evolution and Tinkering. *Science* 196:1161–1166
- Kurakin A (2005) Self-organisation vs. Watchmaker: stochastic dynamics of cellular organisation. *Biol Chem* 386:247–254
- Motomura T (1994) Electron and immunofluorescence microscopy of the fertilization of *Fucus distichus* (Fuciales, Phaeophyceae). *Protoplasma* 178:97–110
- Nick P (2009) Comparing is worth the effort—lessons from mitosis. *Protoplasma* 237:1–2
- Schmid A-MM, Schulz D (1979) Wall morphogenesis in diatoms: deposition of silica by cytoplasmic vesicles. *Protoplasma* 100:267–288
- Stork S, Lau J, Moog D, Maier U (2013) Three old and one new: Protein import into red algal-derived plastids surrounded by four membranes. *Protoplasma*, current issue
- Wang JD, Cao Sh, Du Ch, Chen DR (2013) Underwater Locomotion Strategy by a Benthic Pennate Diatom *Navicula* sp. *Protoplasma*, current issue