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EDITORIAL

Chicken or egg—Weismann revisited

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Multicellularity allows for division of labour. This requires that individual cells adopt different developmental fates. This developmental dichotomy could arise from interactions between the cells, but it could as well be produced by a formative cell division guided by a gradient of developmental determinants within the progenitor cell such that these determinants are differentially partitioned to the daughter cells. It was August Weismann, who, in the attempt to explain inheritance, proposed that the first gonidial division should define the separation of the differentiating, but mortal *soma* from the non-differentiating, but immortal *germ line* as a primordial event of multicellular development (Weismann 1894). Although he could not foresee the concept of differential gene expression at this time, the *soma-germ line* concept has been fruitful to describe early development of the metazoa. Following the Weismann concept, the ultimate cause for cell differentiation and morphogenesis of the daughter organism must be searched in the spatial organisation of the maternal germ line. But how is this internal asymmetry of the germ line cells brought about? For insects, the answer seems to be that it is the maternal tissue that defines the polarity of the oocyte. For instance, the anterior-posterior polarity of the *Drosophila* embryo could be shown to arise from a gradient of maternal, untranslated mRNA for transcription factors such as BICOID, OSKAR and NANOS (St. Johnston and Nüsslein-Volhard 1992). In the same organism, dorsiventral polarity is established from differential activation of the TOLL receptor during oogenesis that, after fertilisation, will drive the transport of the transcription factor DORSAL into the nuclei of the ventral flank (Rushlow et al. 1989). This indicates that the spatial organisation of the insect egg depends on the spatial organisation of the mother—here the chicken is clearly earlier than the egg. However, cell differentiation in organisms with open morphogenesis, where the developmental fate of individual cells is not predetermined by cell lineage, might follow different strategies. Three contributions in the current issue follow spatial organisation before and during the earliest stages of embryogenesis—in the fly *Calliphora* (Anan'ina et al. 2014), in the moscito *Acricotopus* (Staiber 2014) and in the primitive gymnosperm *Encephalartos* (Woodenberg et al. 2014)—and it is interesting to read these contributions in a context:

As shown by the work from the Nüsslein-Volhard lab, the anterior-posterior polarity of the model organism *Drosophila* is controlled by maternal, untranslated mRNA that is integrated into the growing oocyte at specific sites. Thus, the spatial organisation of the maternal germarium and the transport routes in the nurse cells sets the framework for the morphogenesis of the daughter. The work by Anan'ina et al. (2014) in the current issue is focussed on the development of the so-called *ring canals* in the germ line of *Calliphora erythrocephala*, actin-rich structures essential for division synchrony and the differentiation of an oocyte. Previous work from the same group had shown that this phenomenon is essentially conserved between *Calliphora* and *Drosophila*, but due to the larger size, the cell biological aspects are easier to access in *Calliphora* (Kokhanenko et al. 2013). The work arrives on a detailed cellular model that shows how by four mitotic cystoblast divisions a cyst of 16 cells is formed, one of which differentiates into an oocyte. The ring canals are then stabilised in a specific region of the germarium and are mutually shifted by the movement of the cyst to the posterior end of the germarium to give rise to specific branching pattern. This pattern subsequently persists although the cyst increases in size and moves along the ovariole. This process is interesting, because it shows that a cellular movement at a specific developmental time point defines the path along subsequently morphogenetic signals

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(such as maternal untranslated mRNA) will travel and thus control the polarity of the egg.

The Weismann concept relies on a formative cell division that sets up the separation between germ line and soma. This formative cell division should have a structural manifestation. The work by Staiber (2014) in the current issue investigates this aspect for the germ line of the chironomid *Acricotopus lucidus*. Here, the last gonial mitosis separates germ-line chromosomes that migrate without division to one cell pole, whereas the soma chromosomes are retained at the metaphase plane and subsequently divide normally. In the search for the mechanism responsible for this retention, the author investigates the small GTPase Ran that, during interphase, controls nuclear transport, but has been found to control, during mitosis, the nucleation of microtubules attaching to the kinetochore. By immunofluorescence, they can show that Ran accumulates at the kinetochore of the soma chromosomes during this formative division in *Acricotopus*, whereas neither the germ-line chromosomes in the same cell, nor conventional somatic divisions in the same organism or in *Drosophila* show this phenomenon. It is, thus, the specific localisation of Ran that prevents the somatic chromosomes from following their germ line sisters to the cell pole. This intracellular sequestration is crucial for the developmental dichotomy during the subsequent cell divisions.

Whereas these two case studies from insects illustrate the importance of maternal cues for the morphogenesis of the embryo, maternal factors at first sight appear irrelevant in the plant line of evolution. Here, till the fern plants, the meiotic products develop into a so-called gametophyte in complete separation from the maternal sporophyte. This situation changed with the transition to the seed plants, and it is, therefore, interesting to investigate embryogenesis in primitive seed plants. The work by Woodenberg et al. (2014) in the current issue deals with the development of the ovule in the living fossile *Encephalartos natalensis*, a primitive gymnosperm representing an evolutionary stage prevalent around 200 Mya. Here, the zygotic nucleus undergoes numerous free divisions (similar to the situation in *Drosophila*), and these accumulate in the basal region of the proembryo (the free nuclei near the apex degenerate). After around 9–10 rounds of free nuclear divisions, cell walls are formed and the first indications of developmental dichotomy become evident: whereas the basal cells develop into the embryo proper, the apical cells give rise to the suspensor, an embryonic organ responsible for the nutrition of the embryo and doomed to programmed cell death later in development. Interestingly, the seeds are shed from the parent at an early stage of embryogenesis, such that embryogenesis has to proceed for a considerable time separated from the mother plant before a viable embryo is generated. This means that the seed has to be equipped with efficient mechanisms of protection against microbial attack. In fact, non-dehydrated seeds of this species remain viable for up to a miraculous 2 years. The developing meristems (containing the stem cells of the daughter plant and thus the prospective germ line) accumulate tannins correlated with an elaborated endoplasmic reticulum, a feature lacking in the other parts of the embryo. Similar to the situation in the insect germarium, a differential movement (manifest as accumulation of free nuclei in the proembryonal base) is subsequently translated into a developmental dichotomy that gives rise to structural gradients. Thus, although this type of embryogenesis has evolved independently, some of the cellular processes show clear commonalities indicating that the underlying mechanisms must be of very general nature.

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

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