Trends in Plant Science

CellPress

Opinion

(Why) Does Evolution Favour Embryogenesis?

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Complex multicellular organisms typically possess life cycles in which zygotes (formed by gamete fusion) and meiosis occur. Canonical animal embryogenesis describes development from zygote to birth. It involves polarisation of the egg/zygote, asymmetric cell divisions, establishment of axes, symmetry breaking, formation of organs, and parental nutrition (at least in early stages). Similar developmental patterns have independently evolved in other eukaryotic lineages, including land plants and brown algae. The question arises whether embryo-like structures and associated developmental processes recurrently emerge because they are local optima of the evolutionary landscape. To understand which evolutionary principles govern complex multicellularity, we need to analyse why and how similar processes evolve convergently – von Baer's and Haeckel's phylotypic stage revisited in other phyla.

Trends

Complex multicellularity evolved several times independently in eukaryotes.

After 150 years we have some molecular evidence for the hourglass pattern described by Haeckel.

Developmental processes akin to animal embryogenesis are also known in land plants and some other lineages.

Although it involves homologous genes, embryogenesis might not be homologous and it is unclear how and why it evolves.

Haeckel's Theory, and Embryogenesis in Animals and Plants

The 'Biogenetic Law'

Around 150 years ago [1], Ernst Haeckel described that vertebrate **embryos** (see Glossary) resemble each other at a certain stage of development, and that features such as gills come and go during ontogenesis, apparently recapitulating phylogenesis scripted by the evolutionary history of the lineage. The 'biogenetic law' Haeckel described was later transferred into the recapitulation theory or *Biogenetische Grundregel*. Embryos are known from multicellular animals (Metazoa), red and brown algae, and land plants. Such embryos arise from a zygote after fertilisation and possess a 3D body plan characterised by polarity and symmetry breaking. I will use this definition of an embryo throughout, and refer to **embryogenesis** as the early developmental progression from zygote to embryo, typically until developmental arrest or birth. It should be noted that formation of a zygote is not sufficient for embryogenesis, but apparently a necessary prerequisite. Embryogenesis apparently evolved several times independently (convergently), but we do not yet understand the underlying molecular evolutionary principles. After introducing animal and plant embryogenesis, I will discuss the (convergent) evolution of multicellularity and embryogenesis, eventually coming back to Haeckel's ideas to see whether they have a molecular foundation and whether such applies to more than vertebrate embryos.

Animals

Embryogenesis of animals comprises all developmental steps from zygote (generated via gamete fusion) to larval or foetal stages until metamorphosis and birth. After fertilisation, the zygote starts to divide and forms a hollow sphere or disc, the blastula or blastoderm. This process is called cleavage (because the cells divide without increasing their size until the 254-cell stage); translation during this phase is mainly determined by maternal (egg) transcripts. Activation of transcription of the novel diploid genome, created by the fusion of the haploid parental gamete nuclei, as well as cell fate determination, occur only later. At the onset of gastrulation, the primary axis is already established and initially two so-called germ layers form: ecto- and endoderm. Future endodermal cells migrate as single cells or sheets inside the hollow blastula

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http://dx.doi.org/10.1016/j.tplants.2016.02.004

resulting in a two-layered embryo. In Bilateria (encompassing vertebrates), the third germ layer, the mesoderm, forms either from early set-aside cells or following inductive processes from the endomesoderm. Concomitant with induction and the establishment of secondary polarity axes, organogenesis starts. Postembryonic ontogenesis primarily serves organ and thus body growth.

The last common ancestor of the Eumetazoa, uniting the Cnidaria (e.g., sea anemones) with the Bilateria, possessed at least the primary oral–aboral axis, and two germ layers [2,3]. Its gene repertoire already comprised the genes required to establish three germ layers as well as the primary anterior–posterior (head to tail) and secondary dorsal–ventral (back to belly) and left–right axes in the animal lineage crown group Bilateria (Figure 1) [3]. Embryonic development of the Eumetazoa is regulated by the homeodomain (HD) transcription factors (TFs) of the **HOX** family that interact with TALE (three amino acid length extension) HD TFs such as PBC (Table 1 and Figure 1). The HOX hexapeptide (HX) motif, which interacts with TALEs, probably evolved in the last common ancestor of the Eumetazoa [4].

At the basis of the Eumetazoa, the Placozoa already show evidence of germline regulation by HD proteins, for example, by POU (Figure 1) [5]. The next sister lineage are the Porifera (sponges; it should be noted, though, that the basal metazoan branching order is still debated [6]). Sponges possess an apico–basal axis in embryos and larvae, thus axis formation apparently is a **synapomorphy** of the Metazoa (Figure 1). No canonical gastrulation or germ layers *sensu stricto* are observed, but cells are able to migrate and, in some cases, to form epithelia [7,8]. It has been argued from the expression pattern of *Wnt* and *TGF-β* (Table 1) along the embryonic axis that the ability for complex patterning was already present in the last common ancestor of the Metazoa [9,10].

Metazoa, that is, multicellular animals, are thought to have evolved from single-celled organisms akin to Choanoflagellida via colonial forms. The rosette-forming *Salpingoeca rosetta* makes use of conserved Septins to control cytokinesis [11]; a C-type Lectin probably involved in cell adhesion allows this organism to form multicellular colonies [12]. Based on the information derived from the above-mentioned genomes via comparative genomics approaches, animal science has made big steps forward in recent years in unravelling evolution of morphogenesis and thus of body plans.

Plants

The canonical embryogenesis of flowering plants (angiosperms or Magnoliophyta) describes the ontogenesis of the diploid zygote until an arrest (dormancy) occurs that is broken once the seed germinates. The embryo progresses through a globular stage, followed by polarised growth, eventually leading to the heart stage in dicotyledonous plants (possessing two embryonic leaves or cotyledons). During the globular stage, shoot and root apical meristems (SAM/RAM) – and thus stem cells – are formed in the arabidopsis (*Arabidopsis thaliana*) embryo [13]. Several HD TFs are involved in the asymmetric division leading to the globular stage. The expression of WOX HD TFs [14] is already different in the cells of the octant (eight-celled) stage. The embryo suspensor connects the embryo with the maternal (sporophytic) tissues of the developing seed, representing a nutritional (trophic) link.

One could be tempted to compare the progression of the animal zygote to blastula to gastrula with the one of the plant zygote to globular stage to heart stage, and protoderm, root, and shoot apical meristem with the three germ layers of gastrulation. However, shape comparisons are evidently flawed since, for example, monocotyledonous plants do not possess a heart stage. Nutrition of the embryo is taken care of by parental tissue in both lineages (placenta/yolk, endosperm). In contrast to many animals, however, the plant zygote polarises, that is, forms an

Glossary

Aggregative (or colonial) multicellularity: organisms that come into being by aggregation of free living cells, or represent a colony of cells akin to unicellular free living cells.

Alternation of generations: the change between haploid and diploid stages of the life cycle. Both generations have to replicate mitotically (i.e., a zygote is not a generation). All land plants perform alternation of multicellular haploid and diploid generations.

Apogamy and apospory: plant gametophytic (haploid) cells can form haploid sporophyte-like bodies (apogamy), and sporophytic (diploid) cells can form diploid, but gametophyte-like, bodies (apospory).

Apomixis: also known as apomictic parthenogenesis, describes the formation of an embryo from an unfertilised egg cell that has not gone through meiosis. In plants, clonal (asexual) reproduction via an embryo can also occur from other cells than an egg (ectopic), for example, by somatic embryogenesis.

Archaeplastida: monophyletic group comprising organisms that share a primary plastid surrounded by two membranes: the Glaucophyta, Rhodophyta, and Viridiplantae (‘green lineage’, comprising Chlorophyta and Streptophyta).

Clonal (or divisional) multicellularity: an organism that develops by mitotic division of genetically identical cells.

Diplobiont: an organism with two free living stages (e.g., *Ectocarpus siliculosus*, Haptophyta).

Diplont: a diploid organism with all stages of the life cycle being diploid except the gametes (e.g., human, diatoms).

Embryo: to define embryos that have evolved in parallel in different lineages is almost impossible. Here, I use the definition of an embryo as a multicellular structure that arises from a zygote after fertilisation and possesses a 3D body plan characterised by polarity and symmetry breaking.

Embryogenesis: in the sense of this article is the early developmental progression from zygote to embryo, typically until developmental arrest (plants) or birth (animals).