



Bifacial stem cell niches in fish and plants

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Embryonic development is key for determining the architecture and shape of multicellular bodies. However, most cells are produced postembryonically in, at least partly, differentiated organs. In this regard, organismal growth faces common challenges in coordinating expansion and function of body structures. Here we compare two examples for postembryonic growth processes from two different kingdoms of life to reveal common regulatory principles: lateral growth of plants and the enlargement of the fish retina. In both cases, growth is based on stem cell systems mediating radial growth by a bifacial mode of tissue production. Surprisingly, although being evolutionary distinct, we find similar patterns in regulatory circuits suggesting the existence of preferable solutions to a common developmental problem.

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Growing radially – two systems with similar properties

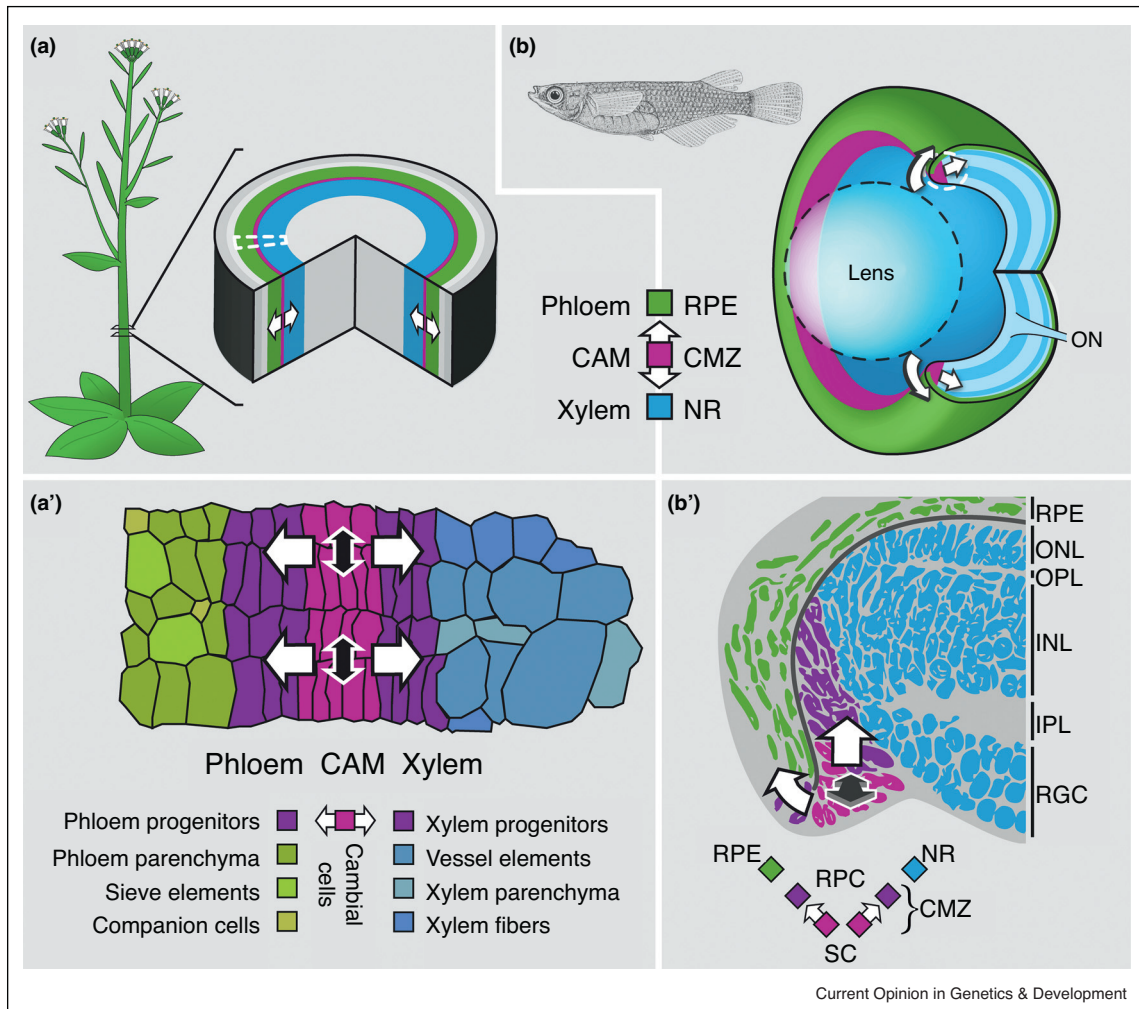
As an exceptional example for the remodeling of adult body structures, shoots and roots of many plant species grow radially. This is to increase mechanical support for their body and to generate additional vascular tissues harboring long-distance transport capacity. The process is mediated by a stem cell niche called the cambium which produces water-transporting cells (xylem, wood) toward the organ center and carbohydrate-transporting cells (phloem, bast) toward the organ periphery [1] (Figure 1(a,a')). Like their differentiated progenies, cells in the cambium are much longer than wide and divide mostly along their longest axis and in parallel to the organ

surface. Thereby, shoots and roots not only expand laterally but, at the same time, the diameter of the cylindrical cambium domain enlarges overall. For example, the total cell number as captured in cross sections from the shoot-to-root boundary in *Arabidopsis thaliana* increases by a factor of 20 within 20 days. Concomitantly, there are 14 times more cambium cells by the end of this period [2]. Tangential expansion of the cambium domain is achieved by symmetric cell divisions perpendicular to the organ surface, thereby increasing the size of the stem cell pool. During tissue formation in radial orientation, xylem and phloem cells expand and acquire a specialized morphology facilitating intra-cellular long-distance transport [3].

Like plants, teleost fish such as medaka (*Oryzias latipes*) harbor the remarkable feature of life-long growth, which is accompanied by continuous growth of their organs. One instructive example is the eye which grows in two phases. During embryogenesis, a lateral out-pocketing of the neural tube forms an optic vesicle which transforms into the bi-layered optic cup (embryonic retina). The lens-facing layer of the optic cup gives rise to the neuroretina (NR) and the lens-averted layer, initially functioning as reservoir for both, NR and retinal pigment epithelium (RPE), eventually forms the RPE (Figure 1(b,b')) [4]. The NR represents the light sensitive, multi-layered tissue composed of one glial and six neuronal cell types [5]. The surrounding RPE is crucial for maintaining the proper performance of photoreceptors in the NR and acts as a light barrier [6]. At the end of embryonic development, a distinct marginal zone of the NR and RPE termed ciliary marginal zone (CMZ) has been established that forms a ring surrounding the lens (Figure 1(b,b')). Distinct stem cells for NR and RPE reside in the CMZ and facilitate postembryonic growth by producing proliferating tissue progenitors [7]. Importantly, NR and RPE progenitors and differentiated cells are separated by the cavity of the ventricle which extends into the retina (gray line Figure 1(b')). Thus, like the cambium, juvenile CMZ-based tissue production follows a bifacial mode adding NR and RPE cells centrally and peripherally to the CMZ (Figure 1(b)). Lateral expansion of the eye is accompanied by an increase in retinal stem cell (RSC) number, the activity of which massively increases the size (cell number) of the retina by a factor of 10 within the first 20 days after initial retinogenesis [7,8**].

In plants, extracellular matrices, the cell walls, prevent cell migration and cause a largely invariant cell arrangement. Strikingly, a similar situation is found in the fish

Figure 1



Schematic overview of the bifacial cambial and retinal stem cell niches of plants and fish.

The geometry of the cylindrical plant stem (here *Arabidopsis thaliana*) and the hemispherical vertebrate eye (here *Oryzias latipes*) is provided by a radial niche of stem cells located inside the tissue. From here, coordinated growth occurs in two directions (centrally and peripherally) giving rise to distinct tissues.

(a–a') For plants, cambial stem cells (CAM, magenta) give rise to central xylem (wood, blue) and to peripheral phloem (bast, green). **(b–b')** In the juvenile fish, retinal stem cells reside in the ciliary marginal zone (CMZ, magenta) producing both, the lens-facing neuroretina (NR, blue) and the lens-averted retinal pigment epithelium (RPE, green) that are physically separated by the cavity of the ventricle (gray line in (b')).

Growth is driven by both, preferential asymmetric cell divisions that result in one stem and one progenitor cell (white arrows, periclinal in plants, radial in fish) and rare symmetric cell divisions to expand the stem cell pool (black arrow, anticlinal in plants, circumferential in fish). Immediate descendants are further subjected to massive proliferation and subsequent differentiation.

(a') In plants, progenitors (purple) on either side of the cambium undergo differentiation into a variety of specialized cell types. **(b')** In contrast, the retinal progenitor cells (RPCs, purple) differentiate into only one cell type in case of the RPE and into six neuronal and one glial cell type for the NR. These are organized in a stereotypical layering (ONL, outer nuclear layer; OPL, outer plexiform layer; INL, inner nuclear layer; IPL, inner plexiform layer; RGC, retinal ganglion cell layer; ON, optic nerve).

a' modified from Ref. [19], with permission from Elsevier

b drawing of adult medaka reprinted from Ref. [45], with permission from Elsevier

retina. To maintain its functionality, it is mandatory that cells – at the time of terminal differentiation – take and retain their position in a pseudo-crystalline arrangement. This arrangement readily allowed revealing clonal relationships. In the cambium recent analyses have demonstrated a bipartite organization of the cambium reflected

by distinct expression domains of cambium regulators [9]. Similarly, lineage analyses in the fish retina following cell transplantation has uncovered a bipartite stem cell niche in the CMZ that is composed of a mixed population of distinct stem cells for either the NR or the RPE [7]. Clonal analyses in the postembryonic NR using inducible

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