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Specification of tapetum and microsporocyte cells within the anther

Dabing Zhang and Li Yang

Flowering plants form male reproductive cells (microsporocytes) during sporophytic generation, which subsequently differentiate into multicellular male gametes in the gametophytic generation. The tapetum is a somatic helper tissue neighboring microsporocytes and supporting gametogenesis. The mechanism controlling the specification of the tapetum and microsporocyte cell fate within the anther has long been a mystery in biology. Recent investigations have revealed molecular switches and signaling pathways underlying the establishment of somatic and reproductive cells in plants. In this review we discuss common and diversified signaling molecules and regulatory pathways including receptor-like protein kinases, redox status, glycoprotein, transcription factors, hormones and microRNA implicated in the specification of tapetum and microsporocytes in plants.

Addresses
State Key Laboratory of Hybrid Rice, School of Life Sciences and Biotechnology, Shanghai Jiao Tong University, Shanghai 200240, China

Corresponding authors: Zhang, Dabing (zhangdb@sjtu.edu.cn, zhangdb3000@gmail.com)

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Introduction

Higher plants differ from animals in forming germ cells within sporophytic tissues late in their development, while animal germ cells arise early in embryos [1]. Reproductive cells in higher plants connect the dominant diploid sporophytic and short haploid gametophytic generations. The sporophytic male reproductive structure, the anther, forms male gametophytes via meiosis and mitosis within the flower [2], and each mature pollen grain released from the parent plant anther contains one vegetative and two sperm cells [3].

In plants, the anther primordium that emerges from the floral meristem usually consists of three layers, L1–L3 [4], with the L1 forming the epidermis, and the L2 differentiating into sporogenous cells (microsporocytes) and three inner somatic cell layers, from outer to inner: the endothecium, the middle layer and the tapetum [5–8]. Unlike the classic model that a single hypodermal cell beneath the epidermis undergoes sequential asymmetric cell divisions to form three concentric rings of somatic layers and germ cells [5,9,10], it was recently recognized in maize that peripheral L2-derived (L2-d) cells undergo asymmetric cell division to form the distinctive two cell types: the endothecium and secondary parietal cell (SPC), then multi-potent SPCs have symmetric cell division forming the middle layer and the tapetum. The central L2-d cells differentiate into enlarged sporogenous cells [11,12••] (Figure 1).

The formation of male meiocytes, gametophytes and gametes relies on the nutritive support of neighboring tapetal cells. Recent investigations revealed the critical role of diverse regulators, such as receptor-like protein kinases and transcription factors, in determining somatic and sporophytic cell fates [13–16]. Several articles reviewed the molecular control on determining somatic and sporophytic cell fates during plant male reproduction [3,5–8,13–16]. In this article, we review and update current understanding of the complex and bi-directional interaction between microsporocytes and tapetal cells, in which diverse factors including receptor-like protein kinases, redox status, glycoprotein, transcription factors and hormones play key roles in specifying the cell lineage and fate of tapetum and microsporocytes in *Arabidopsis thaliana*, rice (*Oryza sativa*) and maize (*Zea mays*).

LRR-RLK signaling promotes tapetal cell identity

Cell surface-localized Leucine-Rich Repeat Receptor-Like Kinases (LRR-RLKs) have been shown to play a conserved and diversified role in determining the identity and numbers of the tapetal cells and meiocytes in plants. *Arabidopsis* CLAVATA1-like LRR-RLKs, BARELY ANY MERISTEM 1 (BAM1) and BAM2 have overlapping functions in regulating the establishment of endothecium, middle and tapetum layers by limiting the expression of SPOROCYTELESS/NOZZLE (SPL/NZZ), a MADS-box transcription factor required for promoting the formation of reproductive and parietal somatic cells [17,18]. *bam1 bam2* double-mutant anthers lack these different cell layers, instead cells interior to the epidermis exhibit features of pollen mother cells (PMCs), suggesting the role of BAM1 and BAM2 in cell fate specification during early anther development [18]. Other LRR-RLKs such as ERECTA (ER)/ERECTA-LIKE 1 (ERL1) and ERL2 and RECEPTOR-LIKE PROTEIN

Figure 1

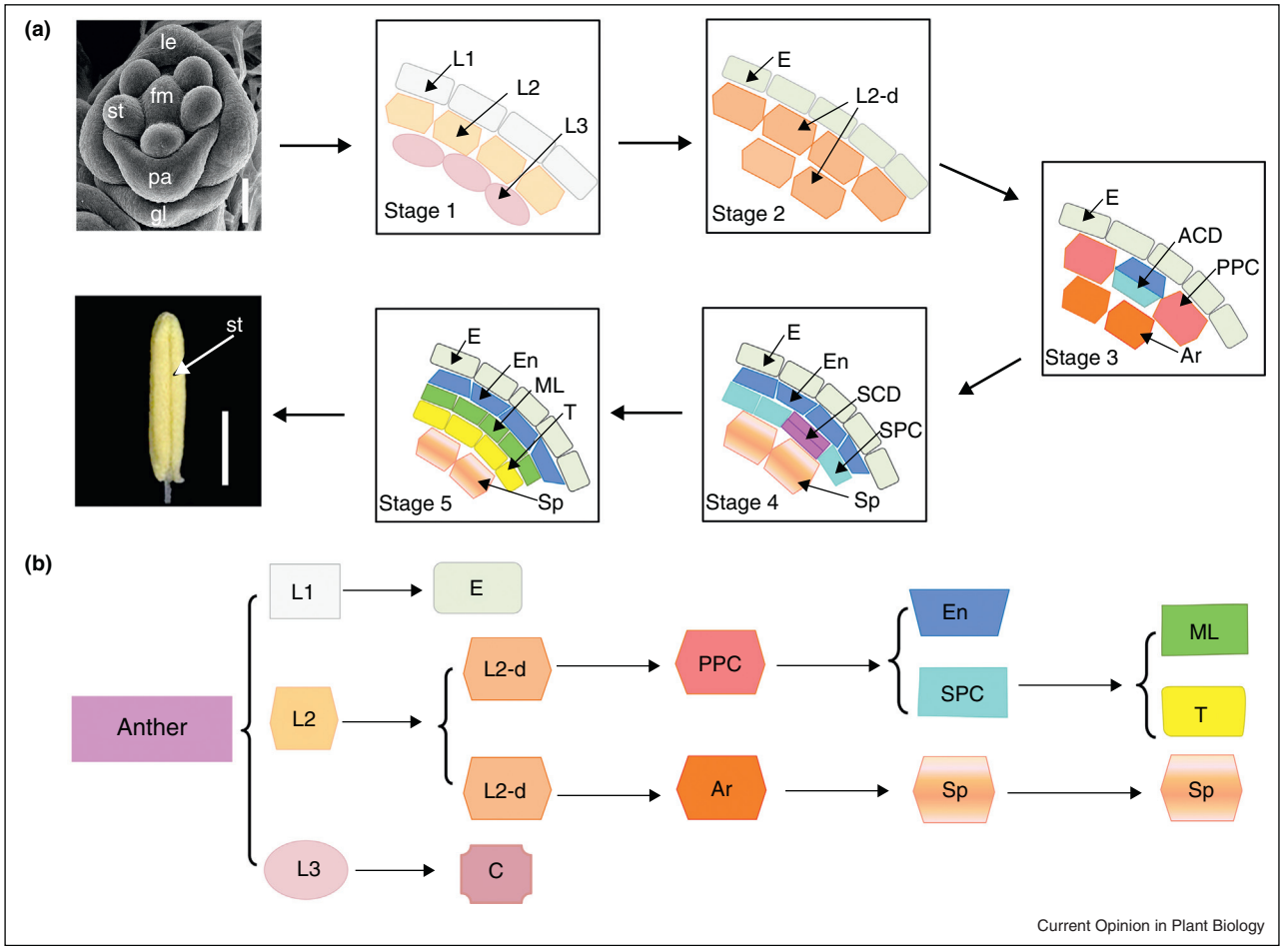

Diagram of cell lineages during early anther development. Floral primordium and mature stamen in **(a)** are from rice. Stage 1–5 of anther development refers to the description by Zhang *et al.* [7]. The anther primordium has the L1, L2 and L3 layers: L1 (ceruse) differentiates into epidermis (E, gray); L2 cells (orange) generate endothecium (En, blue), middle layer (ML, green), tapetum (T, yellow) and sporogenous cell (Sp, purple); L3 (lavender) forms connective tissues **(b)**. ACD: asymmetric cell division; Ar: archesporial cell (orange); C: connective tissue; fm: flower meristem; Le: lemma; L2-d: L2-derived cell (dark orange); pa: palea; PPC: primary parietal cell (crimson); SCD: symmetric cell division; sl: sterile lemma; SPC: secondary parietal cell (cyan); st: stamen. Scale bar: 50 μm (up) and 2 mm (down) in (a).

KINASE 2 (RPK2) were also shown to define anther lobe and early anther cell differentiation [19,20].

In addition, the LRR-RLK complex consisting of EXCESS MICROSPOROCYTES 1 (EMS1, also called EXTRA SPOROGENOUS CELLS [EXS]) [21,22], SOMATIC EMBRYOGENESIS RECEPTOR LIKE KINASE 1 or 2 (SERK1 and SERK2) [23,24], and the putative ligand TAPETAL DETERMINANT 1 (TPD1) [25–27] regulates the cell number of PMCs and specifies tapetal identity. *ems1/exs*, *serk1 serk2*, and *tpd1* mutants exhibit similar defects including no tapetal layer and excess meiocytes as well as aborted meiosis. *TPD1* encodes a small peptide and is mainly expressed in the PMCs [25,26], supporting the model that TPD1 is secreted into the interface between the outer tapetum and inner sporogenous cells, and interacts with the EMS1/EXS and SERK1 and SERK2 forming a receptor complex in specifying cell fate of the tapetal layer [5]. The normal maturation of PMCs in these mutants points out the specification of reproductive cell fate and meiotic initiation independent on somatic tissues even though their microsporocytes cannot finish normal meiosis. Furthermore, although Jia *et al.* [27] confirmed the direct interaction between TPD1 and EMS1 *in vitro* and *in vivo*, it is not clear how this interaction determines tapetal cell fate. Although TPD1 may autonomously suppress the proliferation of archesporial cells, whether there are additional receptors involved in TPD1-mediated somatic-to-germinal switch remains to be elucidated.

Previously it was hypothesized that the microsporocyte might be a default cell identity during precursor cell differentiation, and EMS1 may perceive the signal from