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ORIGINAL ARTICLES

FEMALE ARCHESPORIUM OF ANGIOSPERMS: STRUCTURE, EVOLUTION, AND BIOLOGICAL SIGNIFICANCE

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The review is devoted to the formation of unicellular and multicellular archesporium in female reproductive structures (ovules), differentiation of its cells into megasporocytes, and regulation of these processes. The terminology used in relation to the archesporium is considered, various points of view on the archesporium nature, its place and time of initiation in the ovule and transition into megasporocytes have been analyzed. Based on this, it was concluded that at the early stages of the ovule development, all its cells are identical and meristematic; later, one or more cells in the subepidermal or deeper layers start to differentiate as archesporial (sporogenous) cells, showing differences from other nucellar cells in terms of ultrastructural organization, composition cell wall, characteristics of chromatin in the nucleus.

The differentiation of unicellular and, apparently, multiple archesporium is probably timed to the initiation of the inner integument and is regulated by the expression of the *WUSHEL* (*WUS*), *NOZZLE* (*NZZ*), *WINDHOSE1* (*WIH1*), and *WIH2* genes responsible for cell differentiation in the ovule primordium, and *AINTEGUMENTA* (*ANT*), *BEL1*, *INNER NO OUTER* (*INO*), responsible for the integument initiation. Possible factors leading to the differentiation of several sporogenous cells in the ovule of plants, which are typically characterized by unicellular archesporium (*Arabidopsis*, maize, rice), are considered. These include: mutations in the genes that regulate the differentiation of sporogenous cells; disturbances in epigenetic regulation including the action of small RNAs, DNA methylation and cell cycle mechanisms; as well as irregularities in spatio-temporal coordination of the processes of the ovule development and positional information.

The role of callose in the determination of only one (rarely two) megasporocyte in a multicellular sporogenous complex for its entry into meiosis and the formation of a single gametophyte in the ovule is indicated. It has been suggested that callose not only isolates the megasporocyte for megasporogenesis, but creates a block for the transfer of signaling molecules to neighboring megasporocytes located on the periphery of the sporogenous complex, which stops their development.

The data of the analysis of the evolution of the female archesporium are presented. It has been suggested that the multiple archesporium derived from the unicellular one in the historical development of angiosperms. This is evidenced by the analysis of the distribution of different types of the archesporium among the orders on the APG IV phylogenetic system (2016). The orders of Basal Dicots and Monocots, located at the base of the phylogenetic tree, are characterized by unicellular archesporia (excluding Laurales). The multiple archesporium is characteristic, as a rule, of more advanced orders of Eudicots, but even in these orders and their families, the multiple archesporium does not dominate and appears in fewer species than unicellular one. Sporadic appearance of additional archesporial cells (usually not developing further) in species with the unicellular archesporium, as well as their appearance as a result of mutations, may indicate the secondary nature of multiple archesporium. Probably, multiple archesporium originated as a result of adaptation to preserve reproductive potential of plants, when barriers to the development of a sporogenous cell appear or its frequent death that, apparently, is its biological role.

Keywords: ovule, archesporium, multiple archesporium, sporogenous cell, megasporocyte, megasporogenesis, evolution of the archesporium

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