

STRUCTURE OF SHOOT APICAL MERISTEMS AND PECULIARITIES OF ULTRASTRUCTURE OF THEIR CELLS IN LYCOPHYTES AND FERNS

M. A. Romanova^{a,#}, O. V. Yakovleva^b, A. I. Maximova (Evkaikina)^b,
A. N. Ivanova^{a,b}, and V. V. Domashkina^a

^aSt. Petersburg State University
Universitetskaya Emb., 7–9, St. Petersburg, 199034, Russia

^bKomarov Botanical Institute RAS
Prof. Popov Str., 2, St. Petersburg, 197376, Russia

#e-mail: m.romanova@spbu.ru

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A comparative study of the ultrastructure of cells of the shoot apical meristem (SAM) of monoplex (single apical initial) and simplex (several apical initials) type was undertaken within the discussion on possible ancestral structural type of the SAM for land (higher) plants. The objects of the present study were two lycophytes, a spike moss *Selaginella kraussiana* (Selaginellaceae, Isoetopsida) and a club moss *Huperzia selago* (Lycopodiaceae, Lycopodiopsida), and three species of leptosporangiate ferns: *Pteridium aquilinum* (Dennstaedtiaceae), *Dryopteris carthusiana* (Dryopteridaceae) and *Athyrium filix-femina* (Aspidiaceae). The lycophytes have different the SAM types: monoplex in *S. kraussiana* and simplex in *H. selago*, but similar morphology; all the ferns have monoplex SAM but differ in morphology and growth rhythm. Both monoplex and simplex SAMs of the ferns and lycophytes were composed from surface and subsurface initials (SI and SSI); the SAM of ferns additionally had a so-called cup zone composed of polygonal cells smaller than SIs and SSIs. In the ferns and the spike moss, leaves originated from the SIs; in the clubmoss from a group of SIs and SSIs. Comparing the ultrastructure of the cells belonging to different zones of the monoplex SAM, an approximate number and direction of divisions that occurred during their displacement from the apical initial were additionally estimated. To do this, the attribution of cells to merophytes (successive segments of the apical initial and their derivatives) was defined. In three ferns and a lycophyte *S. kraussiana* it was possible to define the boundaries of four merophytes closest to the apical initial. The number of plasmodesmata per 20 µm of the cell wall was counted in the photographs of the apical initials and their derivatives of *P. aquilinum* using the ImageJ program (NIH, USA). It was revealed that the ultrastructure of the single apical initial in both spike moss and ferns is not unique, but similar to its closest surface and subsurface derivatives. The apical, surface and subsurface initials in the monoplex SAM of all three ferns, in contrast to the same cells of *S. kraussiana*, are characterized by a high degree of vacuolation and a number of ultrastructural features which are atypical for SAM cells, namely the presence of starch grains in plastids located around the nucleus, a large number of lipid droplets in the cytoplasm. The same structural features are characteristic to the cells of cambium suggesting that both types of meristems might share common cell cycle peculiarities with long proliferative quiescence. For the ferns *P. aquilinum*, *D. carthusiana*, and *A. filix-femina*, a relationship between unequal periclinal divisions of surface prismatic cells with shortening of their anticlinal walls and changes in their ultrastructure was established: a decrease in the degree of vacuolation, visual changes in the content of vacuoles. The structure of cup zone cells is typical of meristematic cells: many small vacuoles are located around the nucleus; no starch in plastids or lipids in cytoplasm are detected in these cells. The cup zone cells actively proliferate but loose a capacity for producing leaves. In contrast to ferns, unequal periclinal divisions of the surface prismatic cells of *S. kraussiana* SAM are not correlated with the changes in their ultrastructure. The ultrastructure of the apical initials in the simplex SAM of *H. selago* is typical of meristematic

cells; periclinal divisions of the surface initials are not accompanied by either cell shortening or visual changes in the ultrastructure of the derivatives. The correlation between the number of initials in the SAM, the morphology and the density of plasmodesmata was revealed in both lycopods and ferns: unbranched plasmodesmata with a density an order of magnitude higher than reported for seed plants in the SAM with a single apical initial and significantly fewer branched plasmodesmata in the SAM with several apical initials can be considered to support the viewpoint of the absence of a mechanism of post-cytokinetic plasmodesmata development in plants with monoplex SAM. The ultrastructural differences between the monoplex SAMs of spike moss and four fern species revealed in this study support a hypothesis based on molecular data that meristem with a single apical initial of some lycophytes and most ferns constitutes an independent reversion to the algal ancestor type and have arisen as a result of the loss of the mechanism of secondary plasmodesmata formation in these two lineages. Hence the multicellular apical meristem was among the evolutionary advances of land plants and thus is ancestral for the sporophytes of tracheophytes.

Keywords: monoplex shoot apical meristem (SAM), simplex SAM, apical initial, ferns, lycophytes, plasmodesmata, ultrastructure, evolution

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