Origin and diversification of a MADS-box gene clade associated with the gametophytic generation of land plants.

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Abstract

Land plants are characterized by an alteration of two generations, the haploid gametophyte and the diploid sporophyte. Development of the small and simple male gametophyte of the flowering plant Arabidopsis (*Arabidopsis thaliana*) critically depends on the action of several MIKC* group MADS-box proteins. In this study, MIKC* MADS-box genes were isolated from embryophytes with large and complex gametophyte bodies, the bryophytes. All 11 MIKC* genes of the moss *Funaria hygrometrica*, a close relative of *Physcomitrella patens*, were highly expressed in the gametophyte, indicating that genes of this clade have an evolutionarily conserved gametophytic expression domain. Whereas the gene family expanded in the early-divergent moss *Sphagnum subsecundum*, as it did in *P. patens* and *F. hygrometrica*, only a single homologue is present in the liverwort *Marchantia polymorpha*. Since liverworts are the earliest-divergent land plants, *MpMADS1*, as the gene was called, can be regarded a remnant of the ancestral situation in the land plant lineage. The MpMADS1 protein was shown to form a homodimeric DNA-binding complex, in contrast to the Arabidopsis homologues which are only functional as heterodimeric complexes. Nevertheless, the MpMADS1 homodimer had *in vitro* binding affinities similar to those exhibited by the Arabidopsis heterodimers, and could further partially rescue the pollen defects caused by disruption of the latter. Whereas the functional data indicate that MIKC* proteins have largely conserved biochemical properties, the expression data further imply them as evolutionary conserved regulators of land plant gametophyte development.