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Comment: The Developmental Pattern of Shoot Apices in *Selaginella kraussiana* (Kunze) A. Braun

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## COMMENT

### Comment: The Developmental Pattern of Shoot Apices in *Selaginella kraussiana* (Kunze) A. Braun

Jones and Drinnan (2009) investigated the cellular organization at the apex of the lycophyte *Selaginella kraussiana*. Based on images of fixed meristems, they suggested that a single apical cell with two cutting faces functions as a shoot initial, cleaving by bifurcation to initiate two new shoots. However, if correct, these patterns of division would lead to the formation of particular types of sectors in a clonal analysis where the fates of cells can be followed. Most sectors arising during *Selaginella* development do not conform to the predictions of the model proposed (Harrison et al. 2007). Since clonal analysis is the only unequivocal way to define cell fates, we question the validity of inferring such function and discuss sectors that negate the main conclusions drawn.

Initial cells are stem cells in the growing tips of plant shoots that supply the new cells necessary for growth (Steeves and Sussex 1989). To infer initial fate and cell division patterns in a three-dimensional context, techniques that include a temporal component, such as serial SEM molds, live imaging, or clonal analysis must be used (Poethig 1987). In clonal analysis, single cells are marked in a pulsed genetic perturbation at a particular stage of development. Derivatives of each marked cell divide normally during development, forming a clonal sector and allowing the contribution of individual cells to the body to be determined. The proportion of a fully grown body part occupied by a sector can be used to infer the number of cells that gave rise to that body part. Thus, where a sector occupies half of a fully grown body part, that part arose from two cells. The inference of cell division sequences from clonal sectors is dependent on developmental histology to show whether cell numbers inferred from sectors accurately reflect the number of cells present in developing structures. Thus, neither clonal sectors nor anatomical information alone provides sufficient information for the inference of cell fate (Poethig 1987).

Jones and Drinnan's (2009) article presents anatomical confocal images of fixed apical tissue of *S. kraussiana*. These are used to infer that *S. kraussiana* has a single initial cell at each apex that divides by bifurcation during the initiation of two new branches. Jones and Drinnan present a model of the cell division pattern that occurs. Given the model proposed, a number of sector types should be seen in a clonal analysis of *S. kraussiana*. We discuss sector types predicted by Jones and Drinnan (2009) that relate to initial function (fig. 1) and bifurcation (fig. 2) in comparison to sector types arising in our clonal analysis of shoot development in *S. kraussiana*.

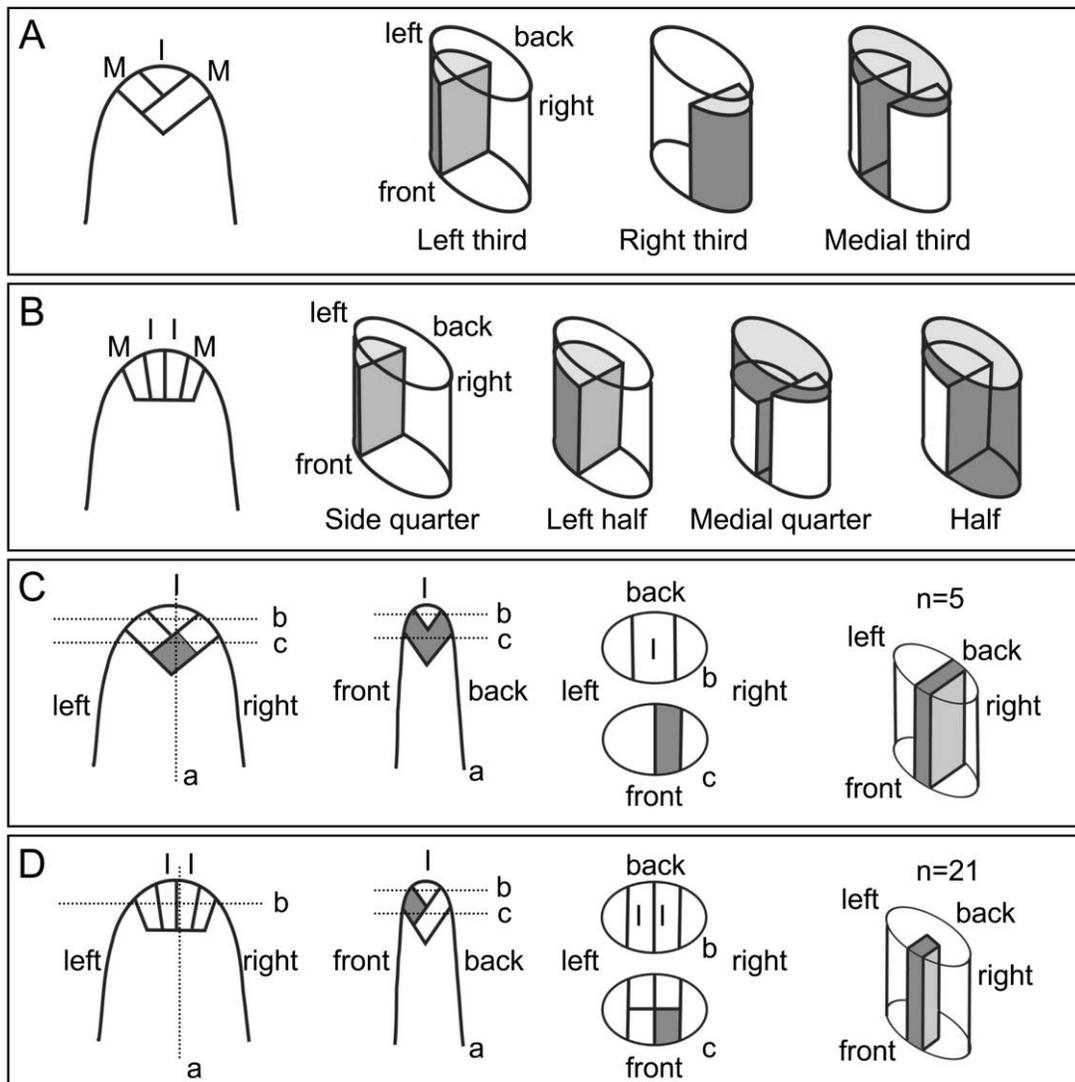
The initial zone in *S. kraussiana* apices comprises large cells that have a lenticular or rectangular surface view, with the longer faces parallel to the sides of the shoot (Harrison et al. 2005, 2007). Given a model of three cells at the apex with a single initial cell dividing to alternate sides to generate

merophyte daughters (fig. 1A), the largest predicted sectors should occupy one-third of the shoot width. Sectors arising from merophytes should occupy a lateral third at either side, whereas sectors arising from an initial should occupy a medial third and go on to occupy the whole shoot. Sectors observed were not consistent with this model. Instead, the largest sectors usually occupied either one-quarter or one-half of the shoot width, suggesting the generative activity of four cells at the apex (fig. 1B). Sectors occupying a medial quarter or half of the shoot width that went on to take over the whole shoot imply that two medial cells have initial fate (Harrison et al. 2007).

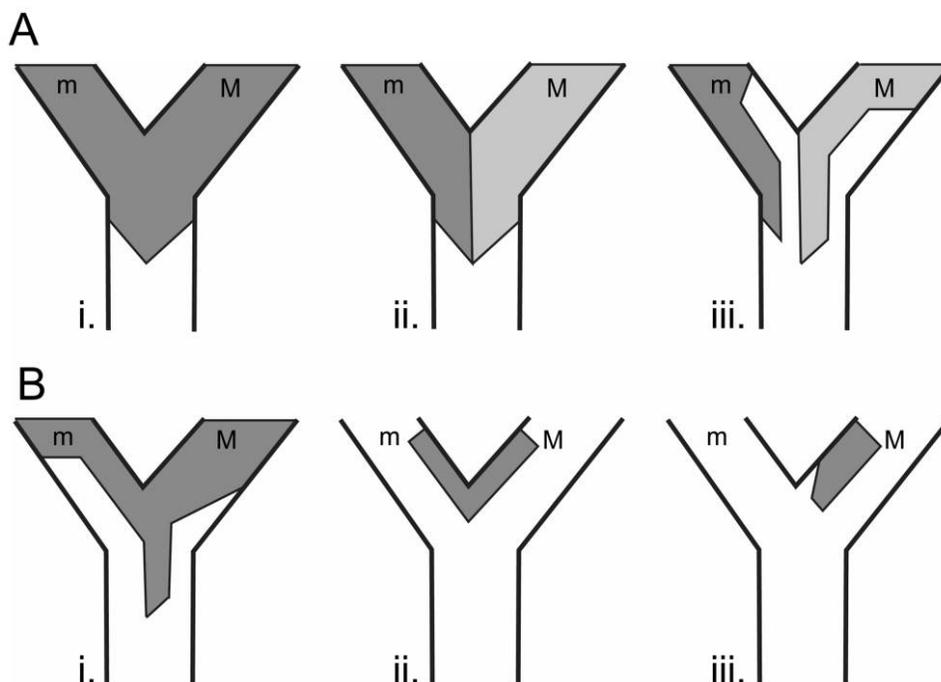
Given a model of periclinal first divisions from merophytes (fig. 1C) as proposed by Jones and Drinnan (2009), predicted sectors arising from each daughter should span the shoot from front to back and occupy about one-quarter of the shoot width. One daughter cell should contribute to a medial portion of the shoot, and a second should contribute to the side of the shoot. Contrary to these predictions, sectors contributing to a medial quarter of the shoot width typically penetrated half of the shoot from front to back (fig. 1D). Those sectors occupying one-quarter of the width of the shoot that spanned the shoot from front to back went on to take over the whole shoot, indicating that they arose from an initial (fig. 1B; Harrison et al. 2007). These sector types are inconsistent with the model proposed by Jones and Drinnan (2009) and indicate that *S. kraussiana* initials cleave to generate merophytes to the front and back of the shoot as well as to the sides.

Clonal sectors around or spanning a branch point are informative about divisions occurring during branching. Jones and Drinnan's (2009) model of a single initial that bifurcates during branching predicts that three main sector types should span the branch point (fig. 2A). Sectors arising from the initial in the parent shoot should occupy the whole shoot and then go on to occupy both daughter shoots. Sectors arising from each new initial should occupy half of the parent shoot and then go on to occupy each daughter shoot. Sectors arising from the first division of each new initial as proposed in Jones and Drinnan (2009) should occupy half of each new shoot, going on to take over each new shoot from left to right. None of these sector types was observed in our study (fig. 2B), and the presence of sectors saddling a branch point (fig. 2B, *ii*) or traversing part of the inner side of a new shoot (fig. 2B, *iii*) negates the proposed model of branching by bifurcation of a single initial cell (Harrison et al. 2007).

In conclusion, although the confocal images presented in Jones and Drinnan's (2009) article offer a novel anatomical view of the *S. kraussiana* apex, they have limited value in inferring initial function. The mechanism of shoot development inferred in our clonal analysis differs in two key ways from that proposed by Jones and Drinnan (2009). First, our data imply that major shoots are generated from two initials. Second, the clonal sectors do not support a model for branching by bifurcation of a single initial (Harrison et al. 2007).



**Fig. 1** Cell division patterns and sectors predicted by Jones and Drinnan (2009) and inferred from clonal sectors by Harrison et al. (2007). *A*, The *Selaginella kraussiana* initial zone and sectors predicted by Jones and Drinnan (2009). A single initial (*I*) cleaves at each side to iterate merophytes (*M*). Sectors predicted to arise from merophytes should occupy approximately one-third of the shoot width spanning the shoot from front to back, whereas sectors predicted to arise from initials should at first occupy a medial third, going on to take over the whole shoot. *B*, The initial zone in *S. kraussiana* meristems as inferred from clonal sectors by Harrison et al. (2007). Sectors that span the shoot from front to back usually occupy one-quarter or one-half of the shoot width, suggesting that there are four generative cells at the apex. Sectors going on to take over the whole shoot can originate from a half shoot sector or a medial quarter sector. Jointly these sectors indicate that there are two initials flanked by merophytes to the sides of the shoot. *C*, Divisions from merophytes and sector types predicted by Jones and Drinnan (2009). Each merophyte cleaves periclinally to generate an inner (gray) and an outer cell. Thus, a sagittal section taken through the dotted line (*a*) would show an initial cell subtended by a single cell that traverses the shoot. Transverse sections across the dotted lines (*b*) would show a single initial cell flanked by two merophytes and (*c*) cells resulting from cleavage of merophytes. Sectors arising from merophyte daughters marked in gray should traverse the shoot as illustrated on the right, and they were seen atypically ( $n = 5$ ). *D*, Divisions and sectors observed by Harrison et al. (2007). Sagittal sections taken along the plane indicated by the dotted line (*a*) indicate alternating cleavage from initials to the front and the back of the shoot generating merophytes (gray). Transverse sections taken across the meristem at levels *b* and *c* show that cells underlying the apex do not span the shoot from front to back. Similarly, shoot sectors of relevant widths do not span the entire shoot unless they go on to take over the shoot ( $n = 21$ ).



**Fig. 2** Sector types relating to initial function during branching. *M* = major shoot, *m* = minor shoot. *A*, Jones and Drinnan's (2009) model of bifurcation of a single initial during branching predicts that sectors initiating at a single point in the stem before a branch point must go on to take over both daughter stems (*i*). Sectors corresponding to mutations in either daughter of the bifurcating apical cell should each occupy half of the parent shoot and one of the daughter shoots (*ii*). Subsequent divisions should give rise to sectors shown in *iii* on the basis that in both branches the left-hand cells arising from the first cleavage of each new apical cell are proposed to be initials (Jones and Drinnan 2009, fig. 4). As such, only sectors in the left-hand side of the shoot can ultimately take over the entire shoot as in *iii*. *B*, Sectors observed in Harrison et al. (2007) negate Jones and Drinnan's hypothesis of branching because sectors arising from an initial do not always occupy the entire parent shoot (*i*). Furthermore, sectors that saddle a branch point (*ii*) or that occupy the inner side of the major shoot (*iii*) were frequent.

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