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Early evolution of the vascular plant body plan — the missing mechanisms

Alexandru MF Tomescu[1], Sarah E Wyatt[2], Mitsuyasu Hasebe[3] and Gar W Rothwell[2,4]

The complex body plan of modern vascular plants evolved by modification of simple systems of branching axes which originated from the determinate vegetative axis of a bryophyte-grade ancestor. Understanding body plan evolution and homologies has implications for land plant phylogeny and requires resolution of the specific developmental changes and their evolutionary sequence. The branched sporophyte may have evolved from a sterilized bryophyte sporangium, but prolongation of embryonic vegetative growth is a more parsimonious explanation. Research in the bryophyte model system *Physcomitrella* points to mechanisms regulating sporophyte meristem maintenance, indeterminacy, branching and the transition to reproductive development. These results can form the basis for hypotheses to identify and refine the nature and sequence of changes in development that occurred during the evolution of the indeterminate branched sporophyte from an unbranched bryophyte-grade sporophyte.

Addresses
[1] Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA
[2] Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA
[3] National Institute for Basic Biology and Department of Basic Biology, School of Life Science, The Graduate School for Advanced Studies, Okazaki 444-8585, Japan
[4] Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, USA

Corresponding author: Tomescu, Alexandru MF (mihai@humboldt.edu)

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Polysporangiophyte origins — the interplay of phylogeny and development

The origin of vascular plants is arguably the most important evolutionary event in the development of the terrestrial biosphere. In modern terrestrial biomes, vascular plants are the dominant source of primary productivity, providing the foundation for virtually all terrestrial ecosystems. Current understanding of phylogeny indicates that vascular plants (tracheophytes) form a monophyletic group [1]. All extant tracheophytes are polysporangiophytes, i.e. plants with branched sporophytes, but the polysporangiophytes also include extinct lineages that did not produce vascular tissue (i.e. xylem with tracheids as conducting elements and phloem) [2]. Early polysporangiophytes had simple sporophytes consisting of undifferentiated, dichotomously branching axes [1,3]. Nevertheless, the evolution of the branched sporophyte paved the way to indeterminate modular growth which, in concert with the evolution of highly specialized conductive tissues (xylem and phloem), led to nutritional independence of the diploid phase. Combined with subsequent evolution of specialized vegetative organs (stems, leaves, roots) these led to the plant sporophyte-sustained ecosystems that are ubiquitous on land today.

Currently, there is intense interest in the origins of polysporangiophytes and vascular plants, which has generated several recent reviews of the topic [4,5•,6••,7••,8•]. Polysporangiophytes, along with the three bryophyte lineages — liverworts, hornworts and mosses — form the embryophyte clade [1,8•,9•]. Although there is wide agreement that polysporangiophytes (including vascular plants) evolved from bryophytic grade embryophytes [1,9•] somewhere between the mid-Ordovician and the mid-Silurian, 450–430 Ma ago [10–13], several aspects of this process remain obscure or are in dispute: the immediate ancestor or sister group of polysporangiophytes; the specific changes that initiated polysporangiophyte origins; the homologies of ancestral polysporangiophyte vegetative organs; the exact evolutionary sequence of changes leading to modern plant structure; and of fundamental importance, the genetic regulatory mechanisms that underlie the changes.

Attempts to answer these questions using a phylogenetic approach — that is, resolve phylogeny and use it to infer steps and mechanisms of evolutionary change, and homologies — have thus far not borne fruit. Despite a plethora of studies employing molecular markers, the phylogenetic relationships between the basal embryophytes lineages (liverworts, hornworts, mosses, and polysporangiophytes) remain largely unresolved [14,15]. Because of the depth of phylogenetic divergences associated with the early stages of embryophyte and polysporangiophyte evolution, as well as the taxon-sampling limitations inherent to molecular phylogenetics [16,17], the phylogenetic approach may never bring full resolution to the basal nodes of embryophyte phylogeny. However, an evolutionary-developmental (evo-devo) approach that first, recognizes what structural changes result from the functional changes of specific genes, second, records the sequence in which comparable structural changes have occurred in the fossil record, and third, screens the genomes of living plants with similar structural features for the presence of orthologues, can provide a framework for formulating testable hypotheses of plant body plan evolution. Such an approach may be better suited for understanding the developmental changes that led to the evolution of polysporangiophytes and, thus, illuminate the homologies of the polysporangiophyte sporophyte.

Hypotheses for the origin of polysporangiophytes

Currently, there are three competing hypotheses for the origin of polysporangiophytes (including vascular plants). Two of these hypotheses are explicit [6••,7••,18••] and a third is implicit from traditional paleobotanical inference and systematic analyses (e.g. [1,3,9•]). All three assert that polysporangiophytes evolved from bryophyte-grade plants and that the ancestral polysporangiophyte had a branching sporophyte which bore terminal sporangia and lacked vascular tissue. However, the three hypotheses differ in the evolutionary mechanisms they predict and the homologies they propose for the axes of the ancestral polysporangiophyte.

Traditional (implicit) hypothesis — branching of a bryophyte-grade sporophyte

The idea that the vascular plant sporophyte originated by increase in length and branching of a bryophyte-grade sporophyte has a long history [19]. This hypothesis, formulated by Campbell [20] and implicit in Bower's [21] discussions of ''the origin of the polysporangiate state'', is reflected in more recent applications, such as models of growth [22] or the coding of morphological characters for phylogenetic analyses (e.g. [1]). However, this 'traditional' hypothesis groups together ideas that are rather diverse and lack specificity. Whereas most of these ideas imply modification of a moss-like sporophyte (e.g. [1,9•,22]), some involve modification of a hornwort sporophyte (e.g. [19]). None of the authors proposes a complete, internally consistent suite of specific changes in development, nor explicit ways to test the hypotheses. Further, specific homologies are not proposed for the vegetative body of the ancestral polysporangiophyte sporophyte. Nevertheless, the implicit ideas denote an upward outlook for morphological evolution (i.e. evolutionary view that interprets evolution/homologies of descendants from characters of ancestors [21]) and in most cases (except for the hornwort-to-polysporangiophyte hypothesis) have the bryophyte seta as the starting point.

Interpolation hypothesis

A second hypothesis (the interpolation hypothesis [18••]) proposes that the polysporangiophyte sporophyte evolved from a bryophytic sporophyte by intercalation of a novel vegetative axial organ between the foot and the sporangium. The hypothesis, as formulated, has a set of correlates that are mutually inconsistent. On the one hand, the hypothesis proposes that intercalation of the vegetative organ occurs early in embryogeny, before sporangial differentiation. On the other hand, the bryophyte sporophyte is seen as a footed sporangium (termed a sporogonium). The seta, when present, is interpreted as an extension and integral part of the sporangium, which implies that the bryophyte embryo expresses only two types of developmental programs — vegetative in the foot and reproductive in the sporangium. Given these constraints (and because the foot has no role in this hypothesis), intercalation of a vegetative organ *before sporangial differentiation* is not possible, except through repression of the reproductive developmental program in the sporangial primordium. Therefore, the vegetative axial organ proposed by this hypothesis is not novel; it is a sterilized sporangial primordium (implicit in Fig. 3 of [18••]). The intercalation hypothesis is, thus, essentially a sterilization hypothesis (see below).

The interpolation hypothesis only implies sporangial sterilization and does not propose specific changes in development with genetic/regulatory origins, thus it is not testable. By proposing that the vegetative organ of the polysporangiophyte sporophyte is a (leafless) stem, this hypothesis suggests homology of the early polysporangiophyte sporophyte with a modern tracheophyte stem. This view corresponds to a downward outlook on evolution (i.e. interpreting the structures of extinct plants by reference to living plants [21,23•]) that goes against the large body of evidence generated by paleobotanical studies over the last two centuries, which demonstrates that the sporophytic axes of early polysporangiophytes differed dramatically from the stems of modern plants in morphology (e.g. absence of leaves and phytomeres), anatomy (e.g. absence of tracheids as water conducting cells, stelar organization, sterome), and branching (apical isotomous) (e.g. [1,3]).

Sterilization hypothesis

Another recent hypothesis [6••,7••] also proposes that the polysporangiophyte sporophyte evolved by sterilization of a sporangial axis. Bolstered by a recent upsurge in support for a hornwort-polysporangiophyte clade in molecular phylogenies (e.g. [24,25]), this sterilization hypothesis explains the evolution of the polysporangiophyte sporophyte from a hornwort-type sporophyte. A key premise of the hypothesis is that, like in hornworts, the embryo of the polysporangiophyte precursor had an upper tier which expressed sporangial identity from its initiation and which developed a basal meristem with indeterminate growth that expressed the sporangial developmental program. Evolution of the polysporangiophyte sporophyte, thus, involved several changes, including (i) a