The evolution of plant development in a paleontological context
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Contrary to what might be expected from the observation of extant plants alone, the fossil record indicates that most aspects of vascular plant form evolved multiple times during their Paleozoic radiation. Opportunity is increasing to unite information from fossil and living plants to understand the evolution of developmental mechanisms and each field can provide tests for hypotheses derived from the other. The paleontological context to recent advances in developmental genetics is reviewed for the evolution of a functionally independent sporophyte generation, of leaves, and of roots — all of which are integral to understanding the explosive radiation of vascular plants during the Devonian, 400 million years ago.

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Introduction
Developmentally minded botanists and paleobotanists have long shared traditions of using an overlapping set of tools to investigate the patterns of cell division and growth that establish final morphology and anatomy [1–7], even if the evolutionary context needed to unite those efforts has not always been available. The study of living plants, however, has progressively been taken in a different direction by technological advances, ranging from the electron microscopy of apical meristems to the molecular revolution, that have encouraged alternative questions regarding organ initiation and identity in a limited number of model species. The wealth of resulting information concerning genetics and earliest ontogeny has been largely inaccessible to paleobotanists, although interest in this challenge has been growing [8–10]. In turn, the fossil record typically has been limited in molecular-based studies to introductory assessments of likely homology and reviving of ideas and imagery from the well intentioned, but unhelpful and misleading [11,12] telome theory.

As sophistication of the molecular understanding of developmental mechanisms has increased, so have the opportunities for rapprochement. For example, the pervasive role of auxin in morphogenesis [13••,14–16] has allowed paleontologists to use vascular patterns preserved in fossils as records of auxin gradients and, thereby, growth dynamics [17–19]. Although the auxin investigations [13••] inspiring this paleontological research have been more classical than molecular, recent advances regarding transient maxima in auxin production and reversibility of auxin pumping ([20–22], reviewed in [23,24•]) will be essential for understanding the more derived vascular patterns of fossil and extant plants. More broadly, differences in morphological disparity between independent derivations of functionally equivalent organs may reflect the constraints of their alternative patterning mechanisms. For example, might such constraints help explain the 420 million years of relative uniformity to lycophyte leaves in comparison to ferns or seed plants? Conversely, the capacity to accommodate the broader anatomical and morphological diversity of fossil and extant plants will be an increasingly important test for any developmental hypothesis proposed based upon model systems (e.g. [25–27]). These applications all require appreciation of the complex diversity of plant form, for which an excellent concise review recently has been published [28••].

Gametophyte and sporophyte
The record of land plant life (Figure 1) commences with a microscopic prehistory extending back at least through the mid-Ordovician (∼470 Ma) of spores and tissue scraps [29•,30,31]. If more complete, these oldest plant fragments presumably would be recognized as of a bryophyte grade of organization and ecology, although not necessarily possessing clear affinity to modern liverworts, hornworts, or mosses. The first macroscopic plant fossils of *Cooksonia* and similar forms (mid-Silurian: ∼425 Ma) consist only of small, determinate, dichotomous axes with terminal sporangia [29•,32]. Although vasculature is absent or equivocal in most of these fossils [29•,32], the capacity for sporophyte branching indicates relationship to the vascular plants — hence, the more inclusive 'polysporangiophytes' for tracheophytes and their tracheid-lacking relatives [33]. The simplest *Cooksonia*-like fossils persisted into the Early Devonian (∼410 Ma), but larger, more complex polysporangiophytes appeared by the Late Silurian [28••,29•,32,33,34•]. With few exceptions [35–38],

Figure 1
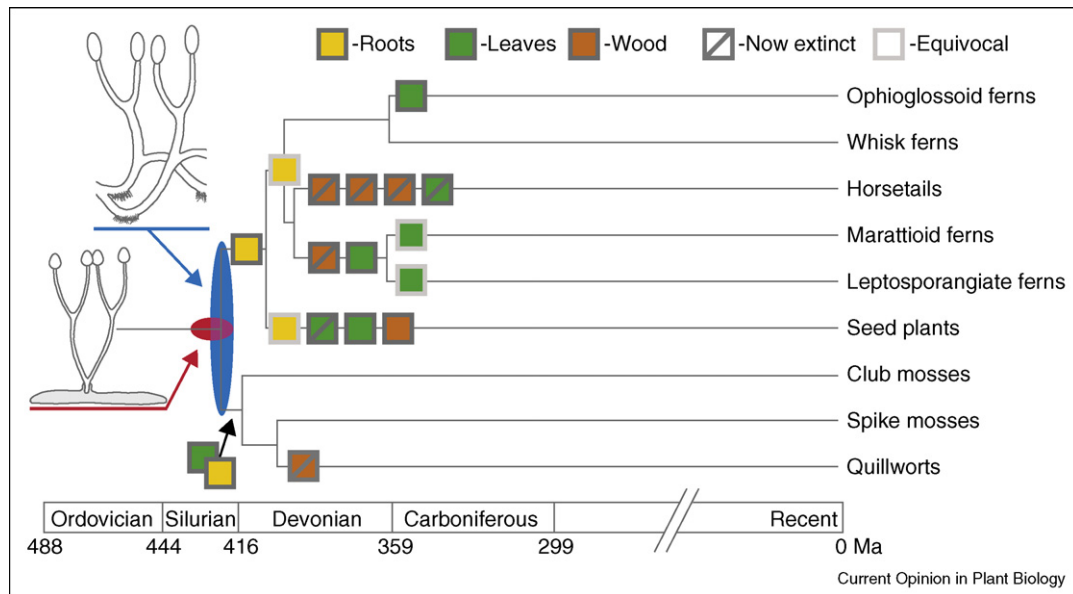
Early radiation of vascular plant form. Boxes on the phylogeny of extant lineages indicate origins of roots (yellow), leaves (green), and wood (brown), including examples that are now extinct (slash). In some cases, the number of origins is equivocal (gray border). Individual lineages may include multiple origins of similar structures, such as leaves in both seed plants and their extinct progymnosperm relatives. Timing of branch points is based on fossil occurrences, including many extinct lineages not shown in the phylogeny. The marattioid/leptosporangiate fern split could be as late as the Early Carboniferous and the ophioglossoid/whisk fern split is poorly constrained by a scant fossil record. The earliest macrofossils (red) are small, determinate, and likely to be gametophyte-dependent for photosynthesis and substrate interaction (hypothetical gametophyte is gray). The common ancestor of extant vascular plants probably had a larger, indeterminate, photosynthetic sporophyte, but was definitely leafless, had no secondary growth, and possessed only axially borne rhizoids rather than true roots (blue). Time scale indicated at the bottom in millions of years before present (Ma).

gametophytes have low preservation potential and are rarely found as fossils.

The phylogenetic nesting of the tracheophytes within the bryophytes and streptophyte algae indicates that the sporophyte was ancestrally small, simple, and physiologically dependent on a dominant gametophyte generation [39]. However, an alternative hypothesis of ancestrally equal (isomorphic) generations has been revived for either tracheophytes or both tracheophytes and bryophytes based on the discovery among Early Devonian polysporangiophytes of gametophytes and sporophytes of nearly equal size and complexity that even include gametophyte stomata and tracheids [28**,33,35]. These isomorphic fossils have been the basis for suggesting that the elusive ancestral gametophyte likely was similar to the oldest sporophyte and, thus, that both generations were small, simple axes resembling *Cooksonia* [33,39].

Expression of *KNOX* and other *TALE* genes is restricted to the sporophyte generation throughout extant embryophytes [40,41] and a diploid-specific role is indicated throughout the green algae/embryophyte lineage by regulation of the haploid to diploid transition in *Chlamydomonas* by TALE heterodimers with sequence homology to those regulating sporophyte meristems in tracheophytes

[41,42•]. Although supporting the multicellular sporophyte as distinct since its inception, this phylogenetic inclusiveness also provides additional examples with the ulvaphyte algae [43] of the evolution of isomorphic generations and, thus, underscores that ancestral for embryophytes need not be ancestral for polysporangiophytes.

Analysis of early sporophyte morphology has provided an alternative approach [44]. All physiological functions must be performed by the axis as the only organ of a *Cooksonia*-like plant, but their axial widths were frequently much less than a millimeter. Such small sizes allow for transport and mechanical support, but are too small for aerated photosynthetic tissue. The sporophyte must have been physiologically dependent upon the unpreserved gametophyte as in bryophytes. Since isomorphic generations under such circumstances would render both gametophyte and sporophyte inadequate for photosynthesis, the ancestral gametophyte must have had a larger size or distinct morphology and the isomorphic generations of some polysporangiophytes represent a derived condition.

Sporophytes too small for physiological independence are dispersed across the polysporangiate phylogeny,

including several nested within the tracheophytes [44]. Because these simple fossils offer so few informative characters, this phylogeny [33] is surely not entirely correct. However, any narrative of sporophyte evolution must be muddled by convergences or reversions because axial diameter, indeterminate growth, sporangial placement, presence of tracheids, and other basic characters are mutually inconsistent [33,44]. Thus, the possibility cannot be disregarded that a physiologically independent sporophyte evolved more than once.

Among extant tracheophytes, the lycophytes are the only possibility of a separate origin of sporophyte independence. Indeed, lycophytes are strikingly large and complex by the Late Silurian, well before equivalent complexity is achieved among euphyllophytes (which includes all living vascular plants aside from the lycophytes) [29•,34•]. If a gametophyte-dependent sporophyte was ancestral for crown group tracheophytes, some genetic trace may be expected. For example, the endodermis in root or rhizome is an important regulator of water and solute uptake. If sporophyte capacity for soil interaction evolved separately in lycophytes, the mechanism for assignment of endodermal identity recently discovered in angiosperms [25] might be expected to be similar in other euphyllophytes, but distinct in lycophytes.

Leaves
Leaves have evolved two [40], four [18], six [45], or more [10] times depending on what characters are emphasized and phylogenetic context. Moss and liverwort enations have a leaf-like form, but with highly divergent anatomy unrelated to tracheophyte leaves. The leaves of lycophyte and euphyllophyte vascular plants are independent convergences because the earliest lycophyte relatives and euphyllophytes are leafless [33]. The extent to which the leaves of various lineages within the euphyllophytes are homologous is ambiguous, but at least some of the more derived aspects of leaf organography evolved independently in different groups [10,18].

Over their long evolutionary history, the morphology of lycophyte leaves is remarkably limited. Aside from a brief diversity of branching forms among Devonian fossils, their leaves have always been linear [28••]. With very rare exception (e.g. [28••,46]), their leaves have always possessed a single unbranching vein. This may well reflect developmental constraint since it certainly does not reflect ecological uniformity: the lycophytes have ranged from arid resurrection plants to submersed aquatics to canopy trees and have fully explored their narrow range of leaf morphological possibilities, including *Selaginella* heteroblasty, the scale-like forms of many taxa, and the fleshy meter long 'microphylls' of Carboniferous trees [28••].

The euphyllophytes do not share leaves as a synapomorphy. Many early forms had determinate lateral branch systems, either three dimensional or planar, which could even be shed as a unit (e.g. [47]), but lacked both lamina and the abaxial/adaxial anatomical organization of leaves. At least these last steps in the establishment of a frond were taken independently in ferns and seed plants [48] and the full complement of leaf traits first appear substantially later among ferns [18,48]. What intermediate characteristics may be homologous between different fern lineages and between fern and seed plant fronds is critically dependent on a poorly understood phylogeny of Devonian and Carboniferous plants [33,49]. Additionally, several extinct tracheophyte groups, including sphenophylls, archaeopterid progymnosperms, and perhaps the noeggerathians [28••], independently evolved simple leaves unlike the compound fronds of ferns and seed plants [18].

Lycophyte and euphyllophyte leaves are thought to have different evolutionary origins. The fronds of ferns and ancestral seed plants are both likely derived from the assumption of a bifacial organization by the determinate lateral branch complexes prevalent among Devonian euphyllophytes [8,10,18,33,45], although such a derivation would not necessarily be shared for the simple leaves of the extinct euphyllophyte clades mentioned above. Lycophyte leaves appear to have evolved from the progressive vascularization of surface emergences on the stem or, perhaps, from sterilized sporangia [28••,33,50].

Expression of the *KNOX* genes that maintain indeterminacy in the apical meristem are repressed by ARP transcription factors in the determinate leaf primordia of a diverse array of seed plants and the lycophyte *Selaginella* [51]. Determinacy is the ancestral sporophyte condition, its suppression for indeterminate growth was an important early innovation, and resumption of determinacy has always been present for the differentiation of sporangia. Thus, even if leaves are independently derived in lycophytes and seed plants, a mechanism for the determinacy of axially borne organs was likely shared from a common ancestor and available for co-option in leaf development [52]. Investigation of *KNOX* and *ARP* expression patterns in sporangia (e.g. [40]) could be informative as the one organ unambiguously homologous across all plants.

Whereas *KNOX* remains repressed in simple seed plant leaves and is upregulated after initial repression in compound seed plant leaves, KNOX is never downregulated in a compound filicalean fern frond [53]. This distinction may reflect fundamentally different genetic mechanisms [10] or similar mechanisms complicated by different evolutionary histories: compound leaves in many extant ferns represent inheritance of an ancestral condition, unlike their secondary derivation in all extant seed plants including cycads. Investigation of derived simple-leaved

ferns may be informative, as could the independent derivations of simple and compound leaves in ophioglossoid ferns.

The antagonistic activity of class III HD-ZIP and KANADI transcription factors involved in the radial patterning of stem vasculature [54•] was co-opted for abaxial/adaxial differentiation of the seed plant leaf [52]. The partial intersection of the leaf primordium with the concentric expression of these genes on the apical meristem provides an intuitive mechanism for how their role in establishing leaf polarity could have evolved [8].

Figure 2
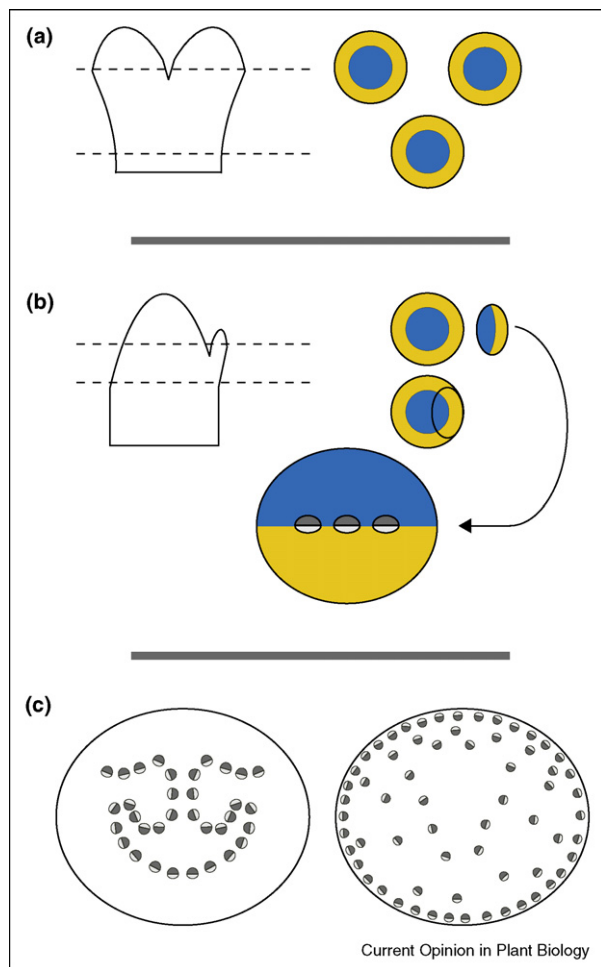
Central (blue) versus peripheral (yellow) axial expression domains of transcription factors, such as *HD-Zip III* versus *KANADI*, can lead to dorsiventrally patterned lateral organs. Axial branching was ancestrally dichotomous **(a)**, but progressively more unequal branching could lead to a monopodial axis bearing small lateral primordia with their partial inheritance of axial positional cues resulting in adaxial/abaxial differentiation **(b)**. Vascular bundles are indicated in the lateral organ section with adaxial xylem (black) and abaxial phloem (gray). It is unclear how such a patterning mechanism could translate to much more complex anatomies, such as those of cycad **((c)**, left) and palm ((c), right) petioles, drawn in simplified cross-section. Diagrams (a) and (b) based upon [8].

An important test will be determining expression patterns in the petiole of a cycad, such as *Dioon* or *Cycas*, where a single boundary between *HD-ZIP III* and *KANADI* expression would be possible albeit extremely convoluted, and a monocot (or, alas, an extinct medullosan seed plant) where the complex distribution of vascular bundles would preclude any clear demarcation (Figure 2). Despite the involvement of *HD-ZIP* genes in lycophyte vascular patterning, they are not involved in establishing lycophyte leaf dorsiventrality [52] — underscoring that other developmental similarities between seed plant and lycophyte leaves represent convergence. That the mechanism of dorsiventral leaf patterning remains unknown in lycophytes and ferns is a symptom of the undersampling of nonseed plants; the seed plants are just one of four to six extant euphyllophyte groups that can be traced back separately to the Devonian along with three lycophyte lineages.

Roots

Roots evolved independently at least in lycophytes and euphyllophytes [34•,50,55]. Root traces first appear in Early Devonian soil horizons, contemporaneous with attached roots in lycophyte-related fossils, but significantly older than the first root-bearing euphyllophytes [29•,34•]. Whether the roots of seed plants and other extant euphyllophytes are homologous is dependent upon an ambiguous phylogeny [33,49].

The root hairs, root cap, and endogenous initiation that all roots share likely have highly divergent evolutionary origins. The universal homology of rhizoids and root hairs is suggested by the ubiquity of filamentous epidermal emergences on gametophytes, rootless Devonian axes, and roots — as has been supported by shared regulation by similar helix–loop–helix transcription factors [56]. Root caps, however, are true convergences that presumably reflect the need for meristem protection during growth through a solid substrate. The repeated evolution of endogenous initiation is striking, but may have been required for the establishment of vascular continuity [50] because dominant auxin transport is away from the apex in stems and toward the apex in roots [57,58]. Since the earliest root-like structures appear to derive from apical dichotomy of the axis [34•], the later first appearance of adventitious roots may date the evolution of endogenous initiation and reversed auxin transport in roots relative to axes.

The limited anatomical disparity of roots relative to stems has been suggested to reflect the more stable soil environment [55]. The more unusual roots certainly are found in environmental extremes like epiphytes and swamp plants, but the greater disparity of axes also reflects their distinct developmental context of tissue patterning based upon proximal auxin transport away from a meristem bearing a diversity of apically produced leaves and other

structures [17]. Conversely, the anatomical homogeneity of roots may reflect the limited possibilities given distal auxin transport toward an apex lacking these structures [50].

Conclusions: a sum larger than the parts

Just as the simple formula of sepal–petal–stamen–carpel would not seem to require 250 000 angiosperm species, progress in understanding the initiation and patterning of sporophyte, root, and leaf cannot fully explain the explosive Paleozoic diversification of vascular plants. Much of the morphological diversity can be attributed to later organ ontogeny (e.g. [5–7]), but equally important will be understanding the evolution of whole plant architecture. Phyllotaxis, branching patterns, and capacity to produce buds [59–62] present more challenges, however, given that the leaves, monopodial growth, and axillary buds of seed plants are unlikely to have direct homologies even among other euphyllophytes.

Finally, the question of secondary growth is invisible with most plant model systems; a mouse may adequately substitute for a rhinoceros in ways that *Arabidopsis* for an oak may not. However, secondary growth was a vital part of the early radiation of vascular plants: wood evolved five or more times by the mid-Carboniferous (~320 Ma) including the lycophytes, basal fern relatives, up to three distinct lineages of sphenopsids, and the progymnosperm/seed plant lineage [4,28**]. Although nearly all evolutions of wood are extinct, the progress in understanding its development [63] need not be limited to seed plants. The extant ophioglossoid *Botrychium* and lycophyte *Isoetes* both possess some secondary tissues [28**,64] and *Equisetum* may preserve genetic trace of its woody ancestry. Fossil anatomy suggests similar developmental mechanisms were involved in each case [19] — here, again, information from a limited extant diversity may be extended by the fossil record.

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