The origin of plants: Body plan changes contributing to a major evolutionary radiation

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Plants (land plants, embryophytes) are of monophyletic origin from a freshwater ancestor that, if still extant, would be classified among the charophycean green algae. Plants, but not charophyceans, possess a life history involving alternation of two morphologically distinct developmentally associated bodies, sporophyte and gametophyte. Body plan evolution in plants has involved fundamental changes in the forms of both gametophyte and sporophyte and the evolutionary origin of regulatory systems that generate different body plans in sporophytes and gametophytes of the same species. Comparative analysis, based on molecular phylogenetic information, identifies fundamental body plan features that originated during radiation of charophycean algae and were inherited by plants. These include, in probable evolutionary order: cellulosic cell wall, multicellular body, cytokinetic phragmoplast, plasmodesmata, apical meristematic cell, apical cell proliferation (branching), three-dimensional tissues, asymmetric cell division, cell specialization capacity, zygote retention, and placenta. Body plan features whose origin is linked to the dawn of plants include: multicellular sporophyte body, histogenetic apical meristem in the gametophyte body, and capacity for tissue differentiation in both sporophyte and gametophyte. Origin of a well-defined sporophytic apical stem cell and a system for its proliferation, correlated with capacity for organ production and branching, occurred sometime between the divergence of modern bryophytes and vascular plant lineages. Roots and their meristem and a multilayered tunica-corpus shoot apical meristem arose later. Regulatory genes affecting shoot meristems, which have been detected by analysis of higher plant mutants, may be relevant to understanding early plant body plan transitions.

Fundamental aspects of the plant body plan are remarkably consistent within the plant kingdom and are different from metazoans. All plants exhibit at least one form of apical meristem consisting of one or more cells that are functionally analogous to metazoan stem cells because they are histogenetic, i.e., able to generate specialized tissues. Plants differ from animals in that the plant apical meristem has the additional capability to generate organs (leaves and stem) and reproductive organ systems (cones or flowers) throughout the life of the plant, whereas the number and form of metazoan organs are embryonically determined. Plants are often described as having a "modular construction" that allows flexibility in organ production in response to changes in environmental conditions. Plants also differ from animals in that the plant sexual life history involves an alternation of two multicellular bodies (sporophyte and gametophyte) that are morphologically different and have changed differently through time. Thus the body plans of these two life history phases have taken separate evolutionary pathways (Fig. 1).

That a simple single-celled histogenetic apical meristem (Fig. 2) appeared very early in plant evolution is suggested by the fact that this type of meristem occurs in modern plants that are considered to be early divergent and not in the green algal ancestors of plants. Early divergent plant forms include bryophytes (liverworts, hornworts, mosses), simple rootless plants considered to lack specialized food and lignified water conducting cells (vascular tissue), as well as simple vascular plants that produce spores rather than seeds. Later-appearing vascular plant groups are characterized by multicellular shoot and root apical meristems. Vascular plants differ from bryophytes in possessing two types of apical meristem, those of the shoot and root. Woody vascular plants possess two additional forms of meristematic tissues, the vascular and cork cambia. Comparative morphology and developmental studies suggest that the apical meristems of gametophytes/sporophytes, bryophytes/vascular plants, and organs/organ systems may be homologous, and that the more complex meristems are derived from simpler forms. Emerging data on genetic control of apical meristem development and function, derived from the study of higher plant mutants that exhibit disruption in meristems (some of which are later described) are expected to allow rigorous testing of these hypotheses.

This article focuses on: (*i*) the earliest stages in the origin of the plant body, including origin of an apical meristem, histogenesis, and essential precursor characters such as the cellulosic cell wall, phragmoplast cytokinetic system, and asymmetric cell division, all of which originated in the ancestors of plants, the charophycean green algae, and (*ii*) transition to the simplest plant body plan. The origin of the plant embryo and other early reproductive innovations have been reviewed separately (1). Higher plant meristems are also covered elsewhere (2).

Fossil and Molecular Evidence Illuminating the Origin of Plants. The origin of terrestrial ecosystems, including the development of modern soils and their biota and emergence of terrestrial metazoan groups, depended on the previous colonization of land by the ancestors of modern land plants. Microfossil evidence (plant spores and cellular scraps) (3–5), when compared with components of modern early divergent plants (6, 7) and considered together with molecular systematic data, indicates that the earliest plants were morphologically similar to modern bryophytes and had appeared by the early mid-Ordovician. Later in the Paleozoic, species-rich communities of rooted vascular plants, including seed plants, appeared (8), producing dramatic effects on atmospheric chemistry and climate (9).

Molecular systematic and other evidence strongly supports the concept that the modern Kingdom Plantae (10), also known as Embryobiota (11) and more informally as land plants, metaphytes, or embryophytes, is a monophyletic group composed of

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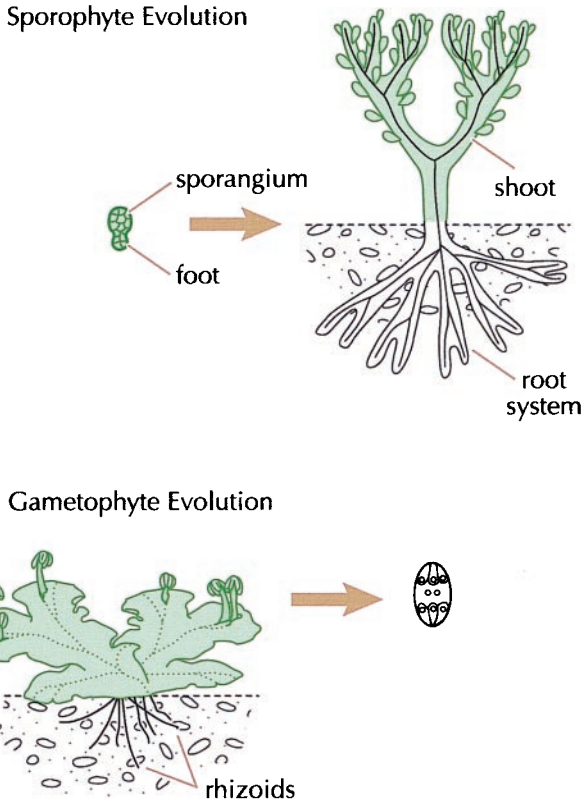

Fig. 1. Diagram showing the different evolutionary pathways (arrows) taken by plant sporophyte (*Upper*) and gametophyte (*Lower*) bodies. Earliest land plant sporophytes probably had a small body consisting of little more than a spore-producing sporangium and foot, a nutritive tissue (*Upper Left*). Early gametophytic bodies were probably larger and more complex, having macroscopic bodies with rhizoids serving anchorage and absorptive functions. Some may have resembled various modern liverworts in having rudimentary conduction systems and erect umbrella-like gamete-bearing structures (*Lower Left*). In contrast, later-divergent vascular plants are characterized by a more complex sporophytic body with specialized shoot and root systems (*Upper Right*) but have few-celled microscopic gametophytes. A female gametophyte, consisting of only seven cells and eight nuclei, which is typical of flowering plants, is diagrammed (*Lower Right*). Thus, through time, the plant gametophyte body has become smaller and less complex, whereas the sporophytic body has become larger and more complex.

early divergent bryophytic groups and later-divergent groups that include some of the bryophytes and vascular plants (tracheophytes) (12). Fossil evidence indicates the existence of several additional extinct lineages (11). The last common charophycean ancestor of land plants is thought to have been related to modern genus *Coleochaete* and order Charales, on the basis of molecular evidence (13, 14) (Fig. 3). Older beliefs that various groups of extant land plants originated independently from different algal ancestors are not supported by the recent data. Phylogeny thus anoints the charophyceans and bryophytes with a special importance in the analysis of early plant evolution and origin of fundamental developmental pathways. Comparative analysis of development in early divergent land plants and charophyceans provides insight into critical body plan and reproductive changes that supported successful radiation of land plants. Such an approach is necessary because fossil evidence bearing on the origin of the first plants is as yet fragmentary and sparse.

Body Plan Changes Associated with the Origin of Plants. The simplest known charophycean morphology (Fig. 4*A*) is represented by the

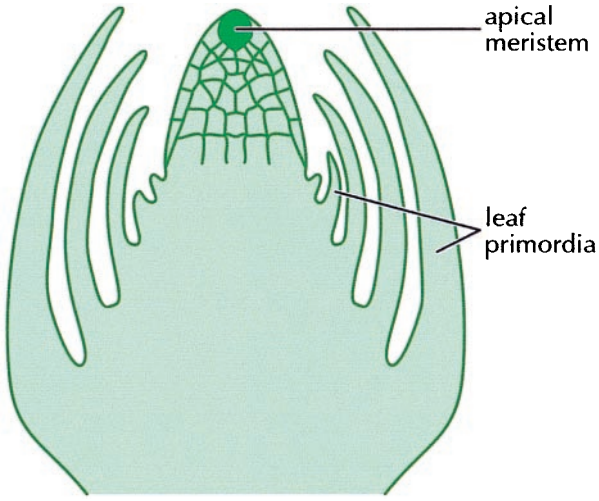

Fig. 2. Diagram of an early type of plant apical meristem, consisting of a single apical stem cell whose progeny form the body tissues. Primordia of leaf-like organs are generated in spiral patterns at the meristem's flanks in ''leafy'' liverworts and mosses, examples of early divergent plants. The apical meristems of modern higher plants differ in being multicellular and layered, but leaf primordia are produced in similar positions.

scaly (wall-less) biflagellate unicell, *Mesostigma*, identified by ultrastructural and some molecular sequence data as possibly the earliest-divergent charophycean (15, 16). Other taxa exhibit simple body types, unicellular nonflagellates, colonies, or unbranched filaments (Fig. 4 *B–D*), composed of cells with cellulosic walls. All of the above-mentioned taxa undergo cytokinesis by furrowing (ingrowth of the cell membrane and cross wall). Phylogeny indicates that this is a plesiomorphic feature for charophyceans. None of these taxa have intercellular cytoplasmic connections, and cell division is not localized into a meristematic region (17).

In contrast, more highly derived charophyceans, Charales and

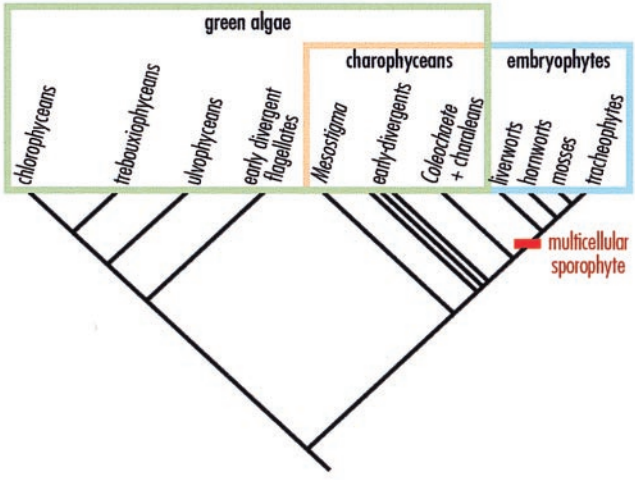

Fig. 3. A model of phylogenetic relationships among green algae (Chlorophyta), charophyceans (Charophyceae), and land plants (embryophytes), based on sequence data for ribosomal, Rubisco, and other genes (references cited in ref. 14). Monophyly of embryophytes is well supported by molecular data and several structural autapomorphies (23), including presence of a multicellular sporophyte. Monophyly of other terminal taxa is less well established, the group labeled ''early divergent flagellates'' (prasinophyceans) is not monophyletic, and the time of *Mesostigma*'s divergence is uncertain.

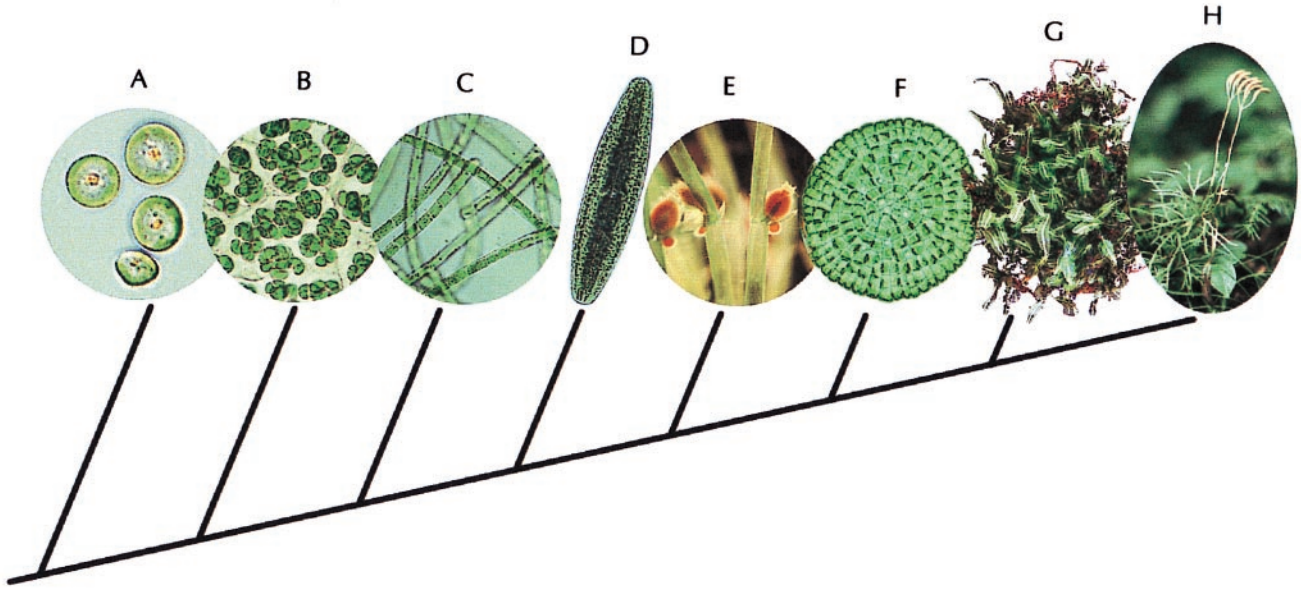

Fig. 4. Increase in body complexity of charophyceans (*A–F*) and early divergent plants (*G* and *H*) is suggested by a phylogenetic model based on molecular data including tubulin (16) and *rbc*L sequences, a gene transfer event, and several intron insertion events (14). (*A*) Unicellular flagellate *Mesostigma* (whose divergence may, however, have preceded that of the charophycean lineage); (*B*) colonial *Chlorokybus*; (*C*) unbranched filament *Klebsormidium*; (*D*) unicellular desmid *Netrium*, belonging to a group (Zygnematales) that also includes unbranched filaments); (*E*) *Chara*, a branched filament with tissue at nodes (indicated by the presence of orange gametangia); (*F*) *Coleochaete*, a planar tissue-like species is shown; (*G*) *Pallavicinia*, representing liverworts, an early divergent plant group; (*H*) *Lycopodium*, an early divergent tracheophyte (vascular plant).

Coleochaete (Fig. 4 *E* and *F*) exhibit: a phragmoplast cytokinetic system of microtubules that is indistinguishable from that of higher plants (18–21); plasmodesmata that provide intercellular links between related cells and that are structurally comparable to plant plasmodesmata (22); complex branched thalli resulting from acquisition of the capacity for a 90° change in the polarity of cell division (17, 23); apical meristematic (stem) cells similar to those of plants but lacking more than two cutting faces (17, 23); tissues consisting of three-dimensional arrays of related cells produced by asymmetric cell divisions in localized areas, although not produced directly by an apical meristem as in land plants (21, 23); cellular specialization within the multicellular body; and the placenta, a structural manifestation of intergenerational communication between the maternal gametophyte and retained diploid generation, which also occurs in land plants (1, 17, 23).

Phylogeny suggests that the above-listed nine features were the basis for derived body plan characteristics regarded as plesiomorphic for land plants and critical to the embryophyte radiation (Fig. 4 *G* and *H*), namely: a gametophytic body composed primarily of parenchymatous tissues having reduced surface area-to-volume ratio and generated by an apical meristemic (stem) cell having three or more cutting faces, and a multicellular sporophyte generation also possessing a histogenetic meristem and having the capacity for complex tissue differentiation (Fig. 4).

(*i*) Cellulosic Cell Wall. The plant cell wall has essential morphogenetic and physiological function in that it determines cell shape and degree of resistance to cell expansion. Phylogenetic systematics and structural variation in cellulose-synthesizing complexes suggest that the cellulosic walls of the charophycean/land plant lineage are not homologous to those of other green algae. An apomorphy of walled charophyceans (+ land plants) is the unique presence of multienzyme cellulose-synthesizing complexes arranged in rosettes of six to eight subunits at the cell membrane. Among charophyceans, such rosettes have been found in *Spirogyra*, *Micrasterias*, *Nitella*, and *Coleochaete*. So far as is known, the cellulose-synthesizing particles of all other cellulose-producing organisms (including the bacterium *Acetobacter*, various algal groups that diverged earlier than green algae, and noncharophycean green algae) are oriented in rows. The geometry of cellulose complexes is directly correlated with size, shape, crystallinity, and intramolecular associations of cellulose microfibrils (24).

Cellulose-containing walls of protists probably evolved multiple times, originating by separate acquisition of cellulose-synthesis genes from endosymbiotic bacteria (24). Alteration in amino acid sequence resulting in change from plesiomorphic linear complexes to apomorphic rosettes might have occurred in as-yet-unknown bacteria or very early in the charophycean radiation. Freeze–fracture transmission electron microscopic studies, coupled with comparative analysis of cellulose synthase gene sequences of early divergent charophyceans, perhaps by using primers based on the RSW1 gene sequence from *Arabidopsis* (25), may be helpful in elucidating the origin of the charophycean/land plant cell wall.

(*ii*) Phragmoplast. The origin of a new mechanism of cell-wall formation during cytokinesis in charophyceans was another dramatic and pivotal event in the origin of the basic land plant body plan. A transitional early phragmoplast has been observed in some zygnemataleans (e.g., ref. 26), and as noted earlier, a cytokinetic system nearly identical to that of land plants is present in advanced charophyceans. At the cellular level, the transition from earlier cytokinesis by furrowing involved (a) the origin of a new type of microtubule array called a phragmoplast, which consists of two sets of parallel microtubles, one set lying on each side of the forming cell wall and oriented perpendicular to the plane of wall development, and (b) a change in the aggregation and binding behavior of cytokinetic vesicles containing pectinaceous wall components such that they fuse with each other, beginning at the center of the cell and moving toward

the cell periphery (17). The molecular basis for these two major cellular level changes is unknown.

(*iii*) Plasmodesmata. These cell membrane-lined channels, containing protein arrays and tubular endoplasmic reticulum, provide a pathway for cytoplasmic communication between neighboring plant cells that are otherwise separated by cell walls. Plasmodesmata are thought to be dynamic, controlling the size of molecules that can pass through them by means of proteins such as myosin, actin, and possibly centrin (27). Because of their ability to regulate molecular traffic, plasmodesmata are considered to be critical to plant development. Several compelling ultrastructural similarities between the primary plasmodesmata of charophyceans (*Chara*) and those of early divergent land plants strongly suggest that these intercellular connections are homologous (22) and that such plasmodesmata were a feature of the earliest land plants. Plant and charophycean primary plasmodesmata are formed during cytokinesis, via enclosure of endoplasmic reticulum by coalescence of surrounding wall vesicles. However, the identity and function of plasmodesmatal proteins and the means by which they become localized is poorly understood.

So far as is known, plasmodesmata appear only in the charophyceans that also generate a phragmoplast at cytokinesis, hence it would seem likely that the phragmoplast was a necessary precursor to the evolutionary origin of primary plasmodesmata in the charophycean lineage. Plasmodesmata have not been found in zygnematalean taxa having only a rudimentary phragmoplast (*Spirogyra*, *Zygnema*, and *Mougeotia*). A survey of the occurrence of primary plasmodesmata and tissue (parenchymatous organization) in eukaryotes suggests that mechanisms for intercellular communication such as plasmodesmata in plants and green and brown algae were necessary, but insufficient by themselves, for the evolution of tissues (28). A more complete understanding of the evolutionary steps involved in the origin of plant plasmodesmata and their functions will require identification of plasmodesma-associated proteins such as calreticulin (29) and analysis of the timing of their evolutionary appearance, which may well have been a staged process.

(*iv*) Branching. The occurrence of branched filamentous advanced charophyceans indicates that their spindle pole organizers have acquired the ability to change angular position. Preprophase plastid migration in *Coleochaete*—a 90° change in the orientation of the large single chloroplast that reflects developmental change in division polarity determinants—is not known to occur in other charophyceans but is characteristic of monoplastidic apical cells of bryophytes and of sporocytes of some vascular plants (30). Acquisition of branching is proposed to have been an early stage in the origin of histogenetic apical meristems in land plants; analysis of genes homologous to those identified as division site determinants in yeasts may illuminate the evolutionary origin of branching in charophyceans and histogenesis in plants (23).

(*v*) Apical Meristems and Asymmetric Cell Division. Among charophyceans, apical growth has been demonstrated only in Charales, which have a single apical cell per shoot, and in *Coleochaete*, where vegetative cell division is restricted to the youngest most peripheral cells. Apical cells in charophyceans have only one (Charales) or at most two (*Coleochaete*) cutting faces and thus generate filaments or planar cell arrays rather than three-dimensional tissues. However, these charophyceans do possess histogenetic cells (capable of dividing asymmetrically and in multiple dimensions), although not located at the apex. These include nodes of charaleans (21) and antheridial initials of *Coleochaete* (17), which generate derivatives in spiral or radial patterns (23).

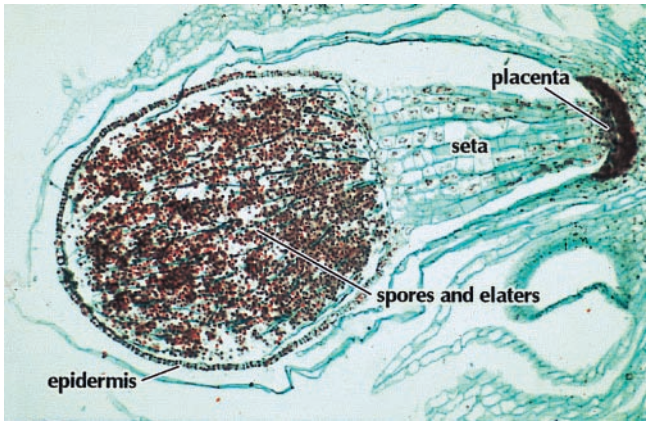

Fig. 5. The multicellular sporophytic body of a liverwort, representing earliest-divergent modern plants, is composed of several tissue types, including resistant epidermis, sporogenous tissues or spores, and specialized dispersal elements known as elaters, supportive seta tissues, and basal tissues whose cells often have typical transfer cell morphology, as do those of the adjacent gametophytic placenta.

In higher plants, asymmetric division is associated with localization of the domain of function of the shoot meristem-specification gene Wuschel (WUS), which is probably a transcription regulator (31, 32). GNOM is a gene expressed during higher plant embryogenesis that is associated with asymmetric cell divisions and polarization leading to differential partitioning of cytoplasmic developmental determinants (33). Mutations (*discordia*) that disrupt asymmetrical divisions in maize leaf epidermis suggest occurrence of a gene that may influence actin-dependent guidance of phragmoplasts (34). A search for homologous genes in advanced charophyceans may illuminate the evolutionary origin of the plant capacity for asymmetric cell division and apical meristematic specification.

(*vi*) Specialized Cells. Although specialized reproductive cells (zoospores, gametes, and zygotes) may occur in early divergent charophyceans, in this green algal class, specialized cells of the vegetative body are limited to *Coleochaete* and Charales. In Charales for example, smaller nodal meristematic cells and very large nondividing internodal cells are generated by asymmetric cell division. Colorless anchoring rhizoids and stipulodes, sharply pointed cells characteristic of the genus *Chara*, are additional examples of specialized vegetative cells. *Coleochaete* is defined by the presence of specialized seta cells that generate long hair-like processes and whose unusual C-shaped plastids may continuously rotate (17). The molecular basis for the origin of cell specialization in the charophycean lineage is unknown.

(*vii*) Placenta. Evidence that chemically mediated developmental signaling between sporophyte and gametophyte phases originated in charophyceans and was inherited by land plants includes production of specialized haploid placental transfer cells near diploid cells, including zygotes of *Coleochaete* and embryos of land plants (Fig. 5). Placental transfer cells are a regular feature of embryophytes, occurring at the gametophyte–sporophyte junction in all plant groups examined, from bryophytes to flowering plants. Such cells with extensive wall ingrowths and increased cell membrane surface area are thought to increase flux of photosynthate across the intergenerational junction and to have been an essential preadaptation for evolutionary origin of the plant embryo. The placenta of *Coleochaete*, hypothesized to be homologous to that of plants, may represent the plesiomorphic form; molecular strategies for testing this hypothesis have been proposed (1).

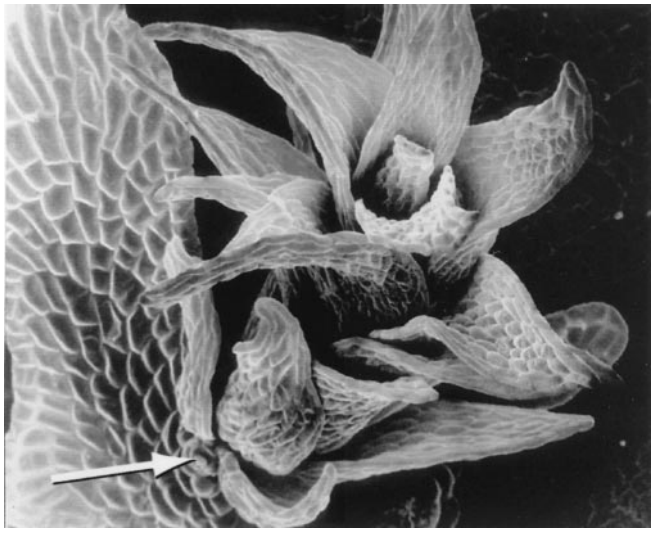

Fig. 6. Scanning electron microscopy view of the two-dimensional plate-like germling stage of the gametophyte body of the early divergent moss *Sphagnum*, which grows by means of peripheral meristematic cells. Also shown is a bud with histogenetic apical meristem that has produced a series of leaf-like organs. The bud develops from one of the peripheral cells (arrow) of the planar stage. Ontogenetically, this moss provides a model of evolutionary transition in apical stem cell capacity, with the planar stage and its simpler meristem representing the precursor type and the bud meristem representing a derived condition.

(*viii*) Body Composed Primarily of Tissue Generated by Apical Meristematic Cell Having Three or More Cutting Faces. The mature gametophytic and sporophytic bodies of plants, including earliest-divergent modern forms (Fig. 5), are composed primarily of three-dimensional tissues, in contrast to charophyceans. This can be attributed to differences in the behavior of apical meristematic cells, i.e., the number of cutting faces. Mature gametophytic bodies of bryophytes are typically generated by an histogenetic apical cell having three or four cutting faces. However, early developmental stages (sporelings, protonemata) may be filamentous, produced by an apical cell having one cutting face, or planar, in which case peripheral cells have two cutting faces, reminiscent of charophyceans. Developmental transition from peripheral apical cells having at most two cutting faces to a single apical cell having multiple cutting faces is best understood in the early divergent moss *Sphagnum* (Fig. 6) (35) and is correlated with developmental appearance of preprophase bands (PPBs) of microtubules, with associated actin (36). In land plants, PPBs typically, although not always (37, 38), mark the site where crosswall development will later commence. The microtubular components of PPBs have not been identified definitively in charophyceans.

Available data suggest that the evolutionary origins of: (*i*) an apical cell having multiple cutting faces in the gametophytic body, (*ii*) preprophase bands, and (*iii*) occurrence of three-dimensional tissue production are linked. These features were likely present in earliest land plants, possibly conferring adaptive advantage if the reduced surface area-to-volume ratio characteristics of tissue resulted in reduced rates of water loss.

(*ix*) Multicellular Sporophyte with Tissue Differentiation. This feature is a unique and defining feature of plants, because (so far as is known) the diploid generation of all charophyceans is unicellular. It is thought to have been derived from the zygote stage of ancestral charophyceans via delay in meiosis and intercalation of a phase of mitotic cell division between syngamy and meiosis (1). Examples of sporophyte tissue differentiation that occurs in even the earliest divergent bryophytes include: (a) a protective epidermis composed of one or more layers of cells that may include tissues specialized for spore dispersal, (b) sporogenous tissues, (c) sterile support tissues located in the sporangial cavity, (d) a basal seta that may lengthen at maturity as a spore dispersal adaptation, and (e) placental tissues in close association with maternal gametophytic tissues (Fig. 5). Genes associated with development of homologous higher plant tissues, such as MERISTEM LAYER1, which encodes a promoter that specifies epidermal expression in meristems and young organ primordia (39), may have homologues in simpler sporophytes.

Sporophytes of most land plants exhibit greater levels of tissue specialization than do gametophytes of the same species. This reflects an uncoupling of body plan evolution in the two phases of the plant life cycle that has persisted through time, culminating in flowering plants, whose sporophytes contain many more cell and tissue types than their gametophytes. Genes that are influenced by changes in ploidy level, such as those recently identified by microarray technology in yeast (40) and *Ceratopteris* MADS6 (a transcription factor expressed in the gametophyte but not the sporophyte) (41), may be responsible for developmental differences in the two plant bodies and should be the target of studies aimed at dissecting the genetic basis for evolutionary uncoupling of body plans in land plants.

The bryophyte sporophyte body, although thought by some to originate from single basal and apical cells (42), has been proposed by others to develop via subapical cell divisions; thus, a typical apical meristem is said to be absent (43). In addition, the bryophyte sporophyte does not proliferate organs. The genetic basis for differences in expression of meristematic activity in bryophyte sporophytes and gametophytes and between bryophyte and tracheophyte sporophytes is unknown.

Body Plan Changes Associated with the Origin of Higher Plants. Major body plan changes occurring between the divergence of modern bryophyte and vascular plant lineages were (*x*) the origin of a well-defined sporophytic apical meristem that allowed the production of organs and (*xi*) the capacity for shoot meristem proliferation, which allowed branching of the sporophyte body in modern vascular plants (tracheophytes) and some fossil groups known as pretracheophytes (12). Sporophyte branching conferred increased body size, productivity, and reproductive potential as well as the capacity to continue growth if some stem cells were damaged or lost (by herbivory, for example). Multiple sporophytic growth points also permitted the specialization of branch systems to form megaphyllous leaves, cones, and flowers. Acquisition of branching contributed to the evolutionary transition toward dominance of the sporophyte body and reduction in size and complexity of the gametophytic body that is characteristic of higher plants (Fig. 2).

A number of genes that encode proteins involved in determining and maintaining the identity of shoot meristem cells have been identified in higher plant systems and are also being sought in earlier-divergent plants. These include MADS genes that encode transcription factors expressed in meristems of the fern *Ceratopteris* and higher plants (41); KNOX and KNAT1 (similar to the Zea knotted-1) homeobox genes (44–47); SHOOT MERISTEMLESS (STM), which keeps meristematic cells from differentiating (31, 48); PINHEAD/ZWILLE, a translation factor associated with meristem identity that may regulate STM expression (49, 50); CLAVATA1 and 3, which oppose STM (51); and CLAVATA 2, encoding a receptor-like protein (52).

Other genes are involved in the developmental transition of shoots from vegetative to reproductive function and thus also influence meristem function. Examples from vascular plants that may also have earlier-divergent homologs include LEAFY (LFY), a transcription factor that induces expression of flower induction genes APETALA1 and AGAMOUS (53, 54) and also

interacts with TERMINAL FLOWER1 (55); FLOWERING LOCUS T (FT), which may encode a membrane-associated protein that is quite similar to mammalian signal transduction pathway proteins (56); CONSTANS (CO), encoding a transcription factor that regulates LFY in response to photoreceptor signals (57); and LUMINIDEPENDENS, which encodes a protein that also regulates LEAFY expression (58). When the sequences in which these genes act (i.e., the structure of developmental networks) become clearer, identification and characterization of ancestral homologues in seedless plants and charophyceans may illuminate the molecular bases for the body plan transformations described in this article.

Summary

Advances in charophycean and seedless plant phylogeny, together with progress in our understanding of the genetic control of meristem determination and function that is derived from analysis of higher plant mutants, set the stage for an improved understanding of fundamental aspects of plant body development and evolution. In this article, we have defined 11 early plant body plan innovations, identified issues that require further study and genes that may illuminate them, and suggested organismal systems likely to prove informative.

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