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Evolution of land plants: insights from molecular studies on basal lineages

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Abbreviations: ABA, abscisic acid; ARF, AUXIN RESPONSE FACTOR; Aux/IAAs, AUXIN/INDOLE ACETIC ACID; ChIP, chromatin immunoprecipitation; CLF, CURLY LEAF; CRISPR, clustered regularly interspaced short palindromic repeat; FIE, FERTILIZATION INDEPENDENT ENDOSPERM; FKF1, FLAVIN-BINDING KELCH REPEAT F-BOX1; FLO, FLORICAULA; GI, GIGANTEA; IAA, indole-3 acetic acid; IPyA, indole-3 pyruvic acid; LFY, LEAFY; Ma, million years ago; NGS, next-generation sequencing; RSL, ROOT-HAIR DEFECTIVE SIX-LIKE; TAA, TRYPTOPHAN AMINOTRANAFERASE OF ARABIDOPSIS; TIR1, TRANSPORT IN-HIBITOR RESISTANT1/AUXIN SIGNALING F-BOX; YUC, YUCCA

The invasion of the land by plants, or terrestrialization, was one of the most critical events in the history of the Earth. The evolution of land plants included significant transformations in body plans: the emergence of a multicellular diploid sporophyte, transition from gametophyte-dominant to sporophyte-dominant life histories, and development of many specialized tissues and organs, such as stomata, vascular tissues, roots, leaves, seeds, and flowers. Recent advances in molecular genetics in two model basal plants, bryophytes *Physcomitrella patens* and *Marchantia polymorpha*, have begun to provide answers to several key questions regarding land plant evolution. This paper discusses the evolution of the genes and regulatory mechanisms that helped drive such significant morphological innovations among land-based plants.

Key words: Terrestrialization of plants; alteration of generations, evolution of development, gene regulatory network

I. The emergence and evolution of land plants

The colonization of land by plants, which may have started as early as the Mid-Ordovician period, approximately 470 Ma, resulted in the establishment of habitable environments on land, and thus promoted an enormous increase in the complexity of terrestrial ecosystems.1) The terrestrialization of animals which followed also depended on this initial diversification and expansion of plants on land.2)

Recent molecular phylogenetic studies indicate that land plants (embryophytes) emerged from a type of freshwater, multicellular green alga that was most likely related to extant Charophyte algae.3,4) Thus, Embryophyta and Charophyta formed a monophyletic group, the Streptophyta, which is a sister group to other forms of green algae (Fig. 1). Among the extant species, three classes of Charophyte algae—Zygnematophyceae, Coleochaetophyceae, and Charophyceae—are considered the closest living algal relatives to land plants, and these groups share many common features, including hexametric cellulose synthases, plasmodesmata, and the presence of phragmoplasts.3,5,6) In fact, it has been hypothesized that ancestral land plants originated from a type of Charophyta green alga, then adapted gradually to life on land, probably through exposure to seasonally-dry or intermediately-moist terrestrial habitats.6-8)

Among the extant taxa of land plants, bryophytes (which include liverworts, mosses, and hornworts) represent the earliest diverging group of terrestrial flora and are considered descendants of some of the very first non-vascular plants.4,9,10) Although phylogenetic relationships among bryophytes are still being debated,4) the morphology of the earliest fossil evidence of land plants (which consists primarily of spore microfossils and tissue fragments from the Middle Ordovician around 470 Ma) suggests that the ancestors of all land plants were, in fact, liverwort-like.11,12) The three extant groups of bryophytes also share several common life history traits, including a dominant haploid gametophyte and a sporophyte that is nutritionally dependent on the gametophyte.[5,13,14)] Their critical position in land plant phylogeny has prompted increased interest in molecular genetic studies of bryophyte species to better understand the evolution of land plant morphology and genomes.

Following the emergence of the bryophytes, vascular plants, or tracheophytes, started to become the dominant vegetation type in terrestrial environments. Fossils of a diverse array of trilete spores found in strata from the Late Ordovician, approximately 443 Ma, suggest that both the origin and diversification of vascular plants had already occurred by that period.[15)] Megafossils of tracheids can be identified in Late Silurian strata from over 415 Ma,[16)] and the life histories of the lycophytes, which are among the oldest extant vascular plants, showcase the dominance of sporophyte generation, as seen in other tracheophytes.[17)] An explosion in the diversity of land plants in general, and vascular plants in particular, occurred during the Devonian period, ca. 415-360 Ma, with many extant groups, including horsetails, ferns, and the first seed plants, emerging and diversifying during this period.[17)]

The evolution of seeds represented yet another critical invention for land plants. This is primarily because, up until that point, it was quite difficult for tiny offspring plants from single-celled spores to survive under the harsh terrestrial conditions present at the time. Seed plants thus evolved a number of adaptations that made it possible for them to reproduce without water. Seed plants have, of course, been widely successful, and have colonized various terrestrial environments and habitats. Gymnosperms first appeared during the Late Carboniferous period, ca. 300 Ma,[17)] becoming a dominant flora sometime between the Permian and the Late Cretaceous, approximately 260-70 Ma. Angiosperms appeared during the Early Cretaceous period, about 100-145 Ma, and began to dominate a majority of terrestrial habitats beginning in the Late Cretaceous, around 100-65 Ma, and continuing until the present day.[18)]

II. Alternation of generations in land plants

The closest living relatives of land plants, the Charophyta algae, have a haplontic life history, where mitosis occurs during the haploid phase, and the only diploid cell that results is the zygote, which then undergoes meiosis to produce haploid spores.[3,7)] In contrast, land plants produce multicellular diploid sporophytes, and thus exhibit a haplodiplontic life history, often described as the alternation of generations. This type of life history consists of two distinct multicellular generations: a haploid gametophyte and a diploid sporophyte (Fig. 2). Interestingly, although alternation of multicellular generations has emerged several times among different groups of algae,[19)] it has evolved only once in the Streptophyta lineage.

Two major theories have been proposed to explain the origins of the alternation of generations in land plants: the transformation (or homologous) theory and the interpolation (or antithetic) theory.[20)] The transformation theory posits that the ancestors of modern land plants underwent an alternation of isomorphic generations, and that morphological differences within each generation arose gradually. This theory was suggested based on the life histories of certain algae, including *Cladophora*, *Ectocarpus*, and *Ulva*, which exhibit distinct multicellular gametophyte and sporophyte generations. In contrast, the interpolation theory postulates that multicellular sporophytes evolved from delays in zygotic meiosis, and the intercalation of mitotic divisions between fertilization and the production of spores via meiosis, resulting in the retention of a diploid multicellular embryo in a gametophytic body. According to this theory, land plant evolution thus proceeded in the direction of progressively more complex sporophytes. In recent years, the interpolation theory has become more widely accepted, in part because of the dominance of gametophytes over sporophytes among bryophytes and the absence of multicellular diploid sporophytes in Charophyte algae.19,21)

Multicellular diploid sporophytes seem to have a better overall capacity for increasing in size and complexity, and their development was one of the most fundamental innovations in terrestrial plant evolution.19) Indeed, in bryophytes, the multicellular sporophyte enables massive spore dispersal, which results in greater genetic variation from a single fertilization event.

Starting from a bryophyte-like ancestor representing the earliest diverging lineages of land plants, the evolution of terrestrial flora has thus proceeded through a progressive reduction in the extent of the haploid gametophyte phase and, in contrast, an increasing dominance of the diploid sporophyte phase (Fig. 2).5) Subsequent innovations that facilitated further adaptations to a terrestrial environment include the formation of stomata, specialized nutrient- and water-conducting cells (vascular tissues), and a sporophytic apical meristem with branching capability; the production of lateral organs (leaves) and specialized underground organs (roots); and the development of seeds and flowers.5,21,22) Such significant body plan transformations prompt the question, “How did land plants acquire the genetic systems that led to such dramatic changes?”.

III. Genetic toolkit for land plant development

Recent advances in genome-sequencing projects involving various Streptophyta lineages, including basal angiosperms,23) gymnosperms,24) lycophytes,25) bryophytes,26) and Charophyta algae,27) have accelerated the identification of both gene losses and acquisitions with regard to land plant evolution. It should be noted that, although genomic information derived from the study of various forms of Charophyte algae, (e.g., orders Charales, Coleochaetales, or Zygnematales) is still rather limited, and only incomplete transcriptome data is currently available,28) the entire genome of the basal Charophyta algae *Klebsormidium* has recently been sequenced.27) Further progress on several genome-sequencing projects in these Charophytes, along with the genomic data gathered from other Streptophytes, will contribute to a better overall understanding of the genetic innovations related to terrestrialization, and the significant transitions among body plans that occurred during the course of land plant evolution.

Some transcriptional regulators, such as KNOX/BELL genes and bHLH genes, have been found throughout the green lineage,[29,30] alluding to its ancient origins. Conversely, some other gene families' encoding transcription factors, such as Class III HD-Zip,[31] Class IV HD-Zip,[32] WOX-type homeodomain proteins,[33] GRAS,[34] and MIKC-type MADS box[35] proteins, are shared among land plants and at least some of the three derived forms of Charophyta algae, but are notably absent in the Chlorophytes. Considerable numbers of transcription factor gene (sub)families, including the VNS (VND-, NST/SND-, SMB-related), have been found exclusively in land plants, but have not been found in the portions of the Charophyta genome sequenced to date,[36] suggesting that acquisition of these new regulatory genes may be correlated with terrestrialization, or related body plan modifications.

Plant hormones perform many critical functions related to the integration of growth, development, and environmental responses in multicellular organisms. Many aspects of plant hormone signaling mechanisms have been well documented in angiosperms,[37,38] but limited knowledge of these processes is available for other green lineages. Similarly, although several plant hormones, including IAA and cytokinins, have been detected in both unicellular and multicellular green algae,[39] their biological functions in algae also remain largely unknown. Recently, comparative genomic and phylogenetic analyses of the signaling components of nine major plant hormones (auxins, ABAs, cytokinins, brassinosteroids, ethylenes, gibberellins, jasmonic acids, salicylic acids, and strigolactones) were conducted using genomic or transcriptome data from 14 plant species, including the red alga *Cyanidioschyzon merolae*, green algae, Charophyta algae, and land plants.[38)] Assuming that the orthologs of these signaling components retained similar functionalities throughout the evolutionary history of plants, these studies propose that auxin-, cytokinin-, and strigolactone-signaling mechanisms first emerged in a Charophyta alga and in some early lineages of Streptophytes, whereas the signaling pathways for jasmonic acids, ABAs, and salicylic acids arose in the last shared, common ancestor of land plants. Thus, comparative genomics suggests that signaling components for different plant hormones seem to have originated at different times over the course of land plant evolution.[38)] It should be further noted, however, that these studies were based on incomplete transcriptome data (not genome-sequence data), for several types of Charophyte algae, as well as for the liverwort *Marchantia polymorpha*, which can only be used for ascertaining the presence (not the absence) of certain gene families. Further genomic sequencing of *M. polymorpha* and other forms of Charophyte algae, along with the functional categorization of these signaling components in some basal plant lineages, will contribute to an increased understanding of the origins and evolution of plant hormone signaling pathways.

IV. Shedding light on land plant evolution via bryophytes

Although comparative genomics, along with phylogenetic and anatomical studies, have produced interesting hypotheses regarding the morphological and physiological evolution of land plants,[40)] functional studies are crucial to testing these theories. Over the last few decades, plant molecular biology has focused primarily on a small number of model angiosperm species, such as *Arabidopsis thaliana*, due to an overall lack of availability and advancement of modern molecular genetic techniques. For example, by the beginning of the 21st century, techniques for transformation and gene targeting had just become available to researchers studying the moss *P. patens*, which had been the sole non-angiosperm model plant used in the investigation of gene functions.[41,42)] More recently, molecular genetic tools have been developed also for the study of the other bryophyte taxon, namely the liverwort *M. polymorpha*.[43-51)] In fact, the sequencing project for the entire genome of *M. polymorpha* has recently been launched under the guidance and direction of the Community Sequencing Program at the Joint Genome Institute (DOE-JGI: http://jgi.doe.gov/why-sequence-a-liverwort/). Of note, this work has already revealed that many of the genes used for regulation of growth and development in other land plants are preserved within the genome, but often show less redundancy. Thus, these two bryophyte models have been used for comparative functional studies of the various genes involved in the evolution of morphological and physiological characteristics among land plants. Some key aspects of the most recent findings from these model systems are discussed next.

IV. i. Evolution of a haplodiplontic life history

One of the most critical innovations in terrestrial plant evolution was the development of a sporophytic apical meristem, which facilitates a complex and indeterminate sporophyte body plan. In angiosperms, the class I KNOX (*KNOX1*) gene family is known to play a key role in the formation and maintenance of meristems within the sporophyte body.52) To this end, the expression and function of all three *KNOX1* orthologs have been examined in *P. patens*, revealing that all *KNOX1* genes in this species are expressed in the apical cell and meristematic region of the sporophyte, and work to regulate the growth potential of the diploid generation, but do not function in the gametophytic meristem.53) This result demonstrates that the *KNOX1*-mediated gene regulatory network for the sporophytic apical meristem is somewhat conserved among land plants, and was likely acquired early on in the evolution of Embryophyta.

Conversely, the disruption of class II KNOX (*KNOX2*) genes in the moss *P. patens* may have resulted in apospory, or the formation of gametophyte-like structures from sporophytes in the absence of meiosis, thus highlighting a critical function of *KNOX2* genes in regard to the repression of gametophytic developmental programming within the diploid sporophyte.54) *KNOX2* functions in angiosperms were later revealed using multiple loss-of-function mutants of KNOX2 in *A. thaliana*. These studies demonstrated that *KNOX2* acts antagonistically with *KNOX1* and modulates the differentiation of all aerial organs in the sporophyte body of *A. thaliana*.55) The KNOX1 and KNOX2 subfamilies most likely originated from a single KNOX gene in an early Streptophyte alga via gene duplication, which enabled these genes to facilitate the development and further evolution of more complex gene regulatory networks in the multicellular diploid sporophyte.

Epigenetic mechanisms are also likely to play a major transitional role in gametophyte and sporophyte growth phases of a plant’s life history. In *P. patens*, homologues of CURLY LEAF (*PpCLF*) and FERTILIZATION INDEPENDENT ENDOSPERM (*PpFIE*) genes encoding subunits of a Polycomb group complex (which controls epigenetic status through chromatin modification) were shown to be essential for the proper establishment of sporophyte and gametophyte identity. To this end, it was discovered that loss-of-function mutants of *PpCLF* and *PpFIE*, would subsequently develop sporophyte-like tissues in the gametophyte growth phase.[56,57)] Thus, these types of studies provide essential clues for understanding the various molecular mechanisms that regulate epigenetic status in the alternation of generations in the life histories of land plants.

IV. ii. Evolution of the auxin system

The phytohormone auxin, an indole-3 acetic acid (IAA), plays a number of pivotal roles in both plant development and environmental response. In the last decade, studies using the angiosperm model *A. thaliana* have revealed the molecular mechanisms that regulate auxin homeostasis, signaling, and transport, as well as the hormone’s function in overall plant development. In angiosperms, a significant amount of IAA is synthesized for the growth and development of the sporophyte from tryptophan (Trp) via indole-3 pyruvic acid (IPyA) by two kinds of enzymes, the TRYPTOPHAN AMINOTRANSAFERASE OF ARABIDOPSIS (TAA) and the YUCCA (YUC) families.58-60) In non-seed plants, it was implicated that the majority of IAA is produced from a Trp-independent pathway, and little is known about the potential contributions of Trp-dependent pathways in basal land plants.61) Recently, molecular genetic studies using the liverwort *M. polymorpha* elucidated that the Trp-dependent IPyA pathway plays a major role in IAA production that is critical for proper growth and development of the gametophyte in this species.62) Homologues of *TAA* and *YUC* genes have also been found encoded in the genome of the moss *P. patens*.26) Studies on two distantly related bryophyte species such as these suggest that the Trp-dependent IPyA pathway for IAA biosynthesis had been already acquired by a common ancestor of land plants, and thus went on to play a significant role in its subsequent life history.

Based on molecular studies in *Arabidopsis*, auxin is known to act by transcriptional regulation through a framework in which auxin receptors (TRANSPORT INHIBITOR RESISTANT1/AUXIN SIGNALING F-BOXs (TIR1/AFBs) target transcriptional co-repressors, AUXIN/INDOLE ACETIC ACIDs (Aux/IAAs), for degradation, thereby releasing AUXIN RESPONSE FACTORs (ARFs) to regulate transcription in auxin-responsive genes.63) Recent functional studies using *P. patens* and *M. polymorpha* have further demonstrated that the molecular mechanisms related to auxin-mediated transcription are essentially conserved among bryophytes and angiosperms.64-67) In angiosperms, large families of genes encode Aux/IAA and ARF proteins, but because individual members often perform redundant functions, uncovering further details regarding these mechanisms becomes rather difficult.68) Regardless, in one study, a transgenic line completely lacking in Aux/IAAs was generated in *P. patens*, which normally only has three Aux/IAA genes. The resulting loss of all three Aux/IAA genes completely conferred an auxin-insensitive phenotype, clearly suggesting that auxin-mediated transcriptional regulation occurs exclusively through Aux/IAA pathways in *P. patens*.69) Other studies recently revealed that *M. polymorpha* also possesses all the required components for auxin-mediated transcriptional regulation with minimal genetic redundancy.66,67) Thus, these two bryophyte model systems are capable of providing good opportunities for investigating principles pertaining to the evolution of auxin actions and its related role in land plant morphogenesis.

IV. iii. Evolution of new tissues and organs

The acquisition of new cell types, including those that form tissues and organs, represents a significant milestone in the evolutionary adaptation of plants to terrestrial environments. Recent comparative genetic studies using both bryophytes and angiosperms indicate potential recruitment of pre-existing gene regulatory networks to regulate subsequent development of novel architectures. For example, the development of root hairs in the multicellular roots of angiosperms is positively regulated by ROOT-HAIR DEFECTIVE SIX-LIKE (RSL) class I genes, which are classified as members of the bHLH VIIIc subfamily.[70] These bHLH members in *P. patens* are known to be involved in the development of rhizoids in the gametophyte generation.[71,72] Additionally, in *M. polymorpha*, an RSL class I gene functions not only in rhizoid formation, but also in the development of gemmae and slime papillae, both of which are differentiated from single epidermal cells.[73] Thus, these results suggest that these bHLH members originally functioned in the gametophyte generation to control the structures derived from single epidermal cells in the common ancestor of land plants, and that these genes were then co-opted for the subsequent development of root hairs in the sporophyte generation of vascular plants.

The development of vasculature was also one of the most critical innovations in the evolution of land plants, as it not only allows for long-distance nutrient and water transport, but also provides rigid structural support for the plant. Vascular plants differentiate these specialized transport tissues within the sporophyte body, and a subfamily of NAC (NAM, ATAF, and CUC) transcription factors, the VNS proteins, plays a key role in the development of water-conducting cells.[36] Although bryophytes are classified as non-vascular plants, some of their lineages do develop specialized cells that conduct nutrients and water in the gametophyte body. Recent studies have also demonstrated that the genetic blueprints for VNS-based transcriptional regulation of cell differentiation related to wall thickening are also conserved in *P. patens*.[74] In fact, the *P. patens* genome has been shown to have eight VNS genes, and triple mutants of these VNS genes have conferred abnormal water-conducting and support cells in the gametophytes. Furthermore, transcriptome analysis of the overexpression of the PpVNS7 gene in *P. patens* indicates that PpVNS regulates many of the putative orthologs of the direct targets of VNS in *Arabidopsis*.$^{74)}$ Thus, the combined results of these studies indicate that transcriptional regulation and cellular functions of water-conducting cells are conserved in the evolutionary lineages between *P. patens* and *A. thaliana*, suggesting that the acquisition of the NAC-mediated machinery for development of water-conducting cells was critical to the successful adaptation of plants to land.

Photoperiodic control in the transition from vegetative to reproductive growth phases is also crucial for land plants. In angiosperms, GIGANTEA (GI) and FLAVIN-BINDING KELCH REPEAT F-BOX1 (FKF1) form a protein complex that plays a critical role in the regulation of photoperiodic flowering. Kubota et al. (2014) revealed the existence of GI and FKF1 orthologs in *M. polymorpha*, and demonstrated their essential roles in the photoperiodic control of growth phase transitions in the gametophyte.$^{75)}$ The presence and function of the GI-FKF1 complex within liverwort lineages suggest that this system had already been previously acquired in the common ancestor of land plants as a means of regulating reproductive phase transitions in the gametophyte generation. Thus, the GI-FKF1 system was most likely co-opted during the course of land plant evolution to regulate reproductive phase transitions in the sporophyte generation of vascular plants.

Conclusion and future perspectives

Following the completion of the human genome project in 2003, enormous progress has been made in DNA-sequencing technologies, especially concerning the development of next-generation sequencing (NGS) techniques. This has not only resulted in decreased costs per megabase, but also produced an overall increase in the number and diversity of sequenced genomes. As discussed previously, various green lineages have been sequenced, and this has accelerated the identification of both gene losses and acquisitions throughout the course of evolution in land plants. Future progress in genome sequencing, especially in Charophyta algae, bryophytes, and basal vascular plants, will also help promote the use of comparative genomics in understanding plant taxa and refining their phylogenetic relationships. In addition to whole-genome sequencing techniques, NGS technology has also been applied in a variety of contexts, including transcriptome, ChIP-seq, and methylation procedures. Comparative genomics using such NGS applications will help provide new insights regarding the evolution of gene regulatory networks in plants.

Exploration of the evolutionary path in land plants is indeed challenging, because many lineages containing informative intermediate traits are extinct, e.g. Polysporangiophytes, the transitional fossil plants between the non-vascular bryophytes and the vascular plants, of which sporophyte has branching stems with no vascular tissue. At present, the majority of gene function data has been available exclusively in angiosperms, the most recently diverged plant lineage. However, as highlighted in this article, functional studies in the non-angiosperm models *M. polymorpha* and *P. patens* have started to provide valuable opportunities for testing key hypotheses regarding land plant evolution. Further development of experimental systems for molecular analyses in various extant Streptophyta lineages will contribute to our understandings on the evolution of underlying genetic regulatory mechanisms. New genetic transformation techniques have recently been developed with respect to other, non-angiosperm lineages, including ferns$^{76,77)}$ and Charophyta algae.$^{78,79)}$ Powered by the recently established genomic modification technology known as the CRISPR (clustered regularly interspaced short palindromic repeats) / Cas9 system,$^{80)}$ functional genomic studies among various Streptophyte lineages will also provide opportunities to investigate the functions of genes hypothesized to be involved in the evolution of land plants.

Recent studies have revealed that regulatory genes have often existed before the emergence of the morphological structures that they control. For example, the FLORICAULA (FLO)/LEAFY (LFY) genes, which are transcription factors critical for flower development, are also found in non-flowering Streptophytes (i.e., gymnosperms, ferns, lycophytes, bryophytes, and Charophyta algae).$^{81)}$ In *P. patens*, two *LFY* genes redundantly regulate the first cell division after formation of the zygote.$^{82)}$ Gene duplication is thought to be the common mechanism of neofunctionalization, as it generates additional gene copy that may acquire new functions, and the remaining copy can cover the function of the original gene. However, *LFY* exists as a single-copy gene in most plants, with the exception of gymnosperms where a *LFY*-like paralog, *NEEDLY*, emerged after a major duplication event. While remaining a highly conserved and essential single-copy gene, *LFY* underwent changes to its DNA binding specificity, acquired new downstream target genes, and shifted the developmental function in the course of land plant evolution.81) Thus, it is likely that regulatory genes were recruited from pre-existing functions to control the development of novel architectures. Because many regulatory genes related to sporophytes of angiosperms have their homologues in basal plants whose life histories are gametophyte-dominant, increases in morphological complexity of the sporophyte body could be caused by, at least in part, the co-option of the regulatory genes for gametophytes to the sporophytes.21) Further functional genomic studies in diverse Streptophyta lineages, including the liverwort *M. polymorpha*, should shed light on the co-option and reassembly of gene regulatory networks throughout the evolution of land plants.

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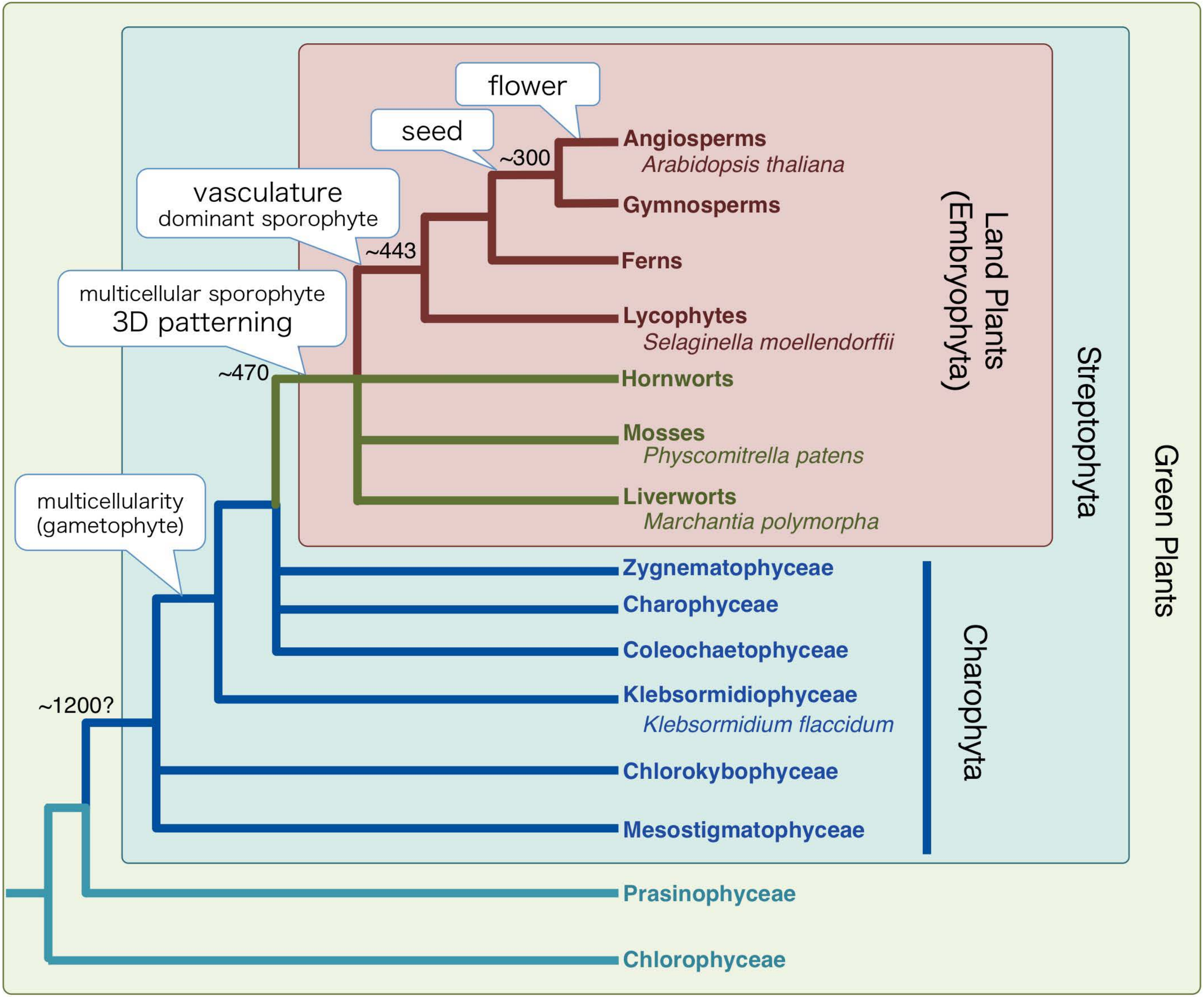
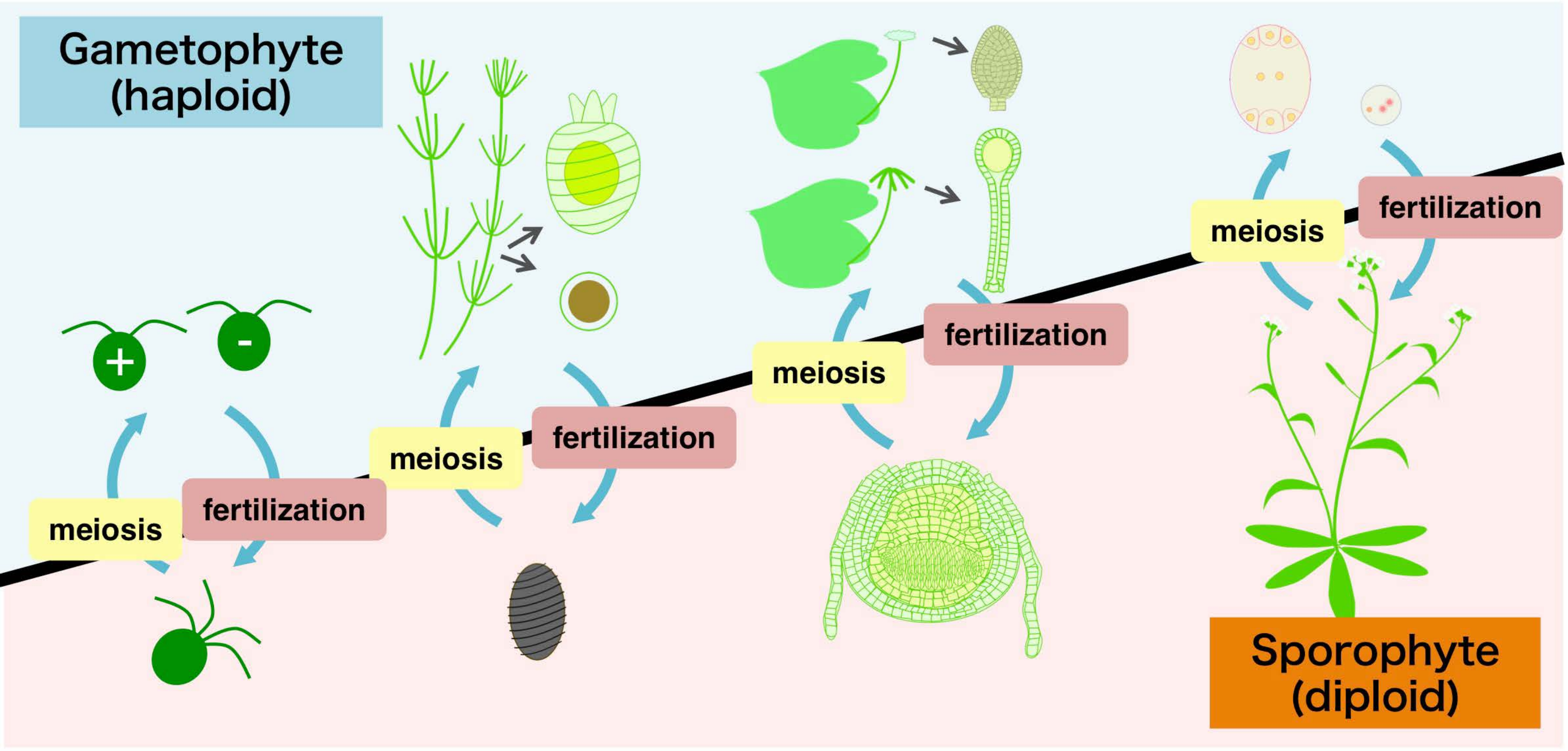
Figure legends

Fig. 1. Phylogenetic relationships between major groups of extant green plants. Key morphological innovations that occurred during plant evolution are indicated. Estimated dates for some nodes are listed in millions of years before present.

Fig. 2. Alternation of generations and the evolution of land plants. Chlorophycean and Charophycean algae do not have a multicellular sporophyte generation, as their zygotes undergo meiosis directly following fertilization. In contrast, both gametophyte and sporophyte generations in all land plants are multicellular, with their life cycles demonstrating alternation of generations. The multicellular diploid plant (sporophyte) produces spores through meiosis, whereas the multicellular haploid plant (gametophyte) develops from spores and gives rise to haploid gametes through mitosis. In bryophytes, including liverworts and mosses, the dominant generation is haploid. The opposite is true for vascular plants (tracheophytes), in which the diploid generation is dominant and the sporophyte comprises the main plant.


flower
seed
~300
Angiosperms
Arabidopsis thaliana
Gymnosperms
vasculature
dominant sporophyte
~443
Ferns
multicellular sporophyte
3D patterning
Lycophytes
Selaginella moellendorffii
~470
Hornworts
Mosses
Physcomitrella patens
Liverworts
Marchantia polymorpha
Land Plants
(Embryophyta)
Streptophyta
Green Plants
multicellularity
(gametophyte)
Zygnematophyceae
Charophyceae
Coleochaetophyceae
Klebsormidiophyceae
Klebsormidium flaccidum
~1200?
Chlorokybophyceae
Mesostigmatophyceae
Charophyta
Prasinophyceae
Chlorophyceae



Gametophyte (haploid)

+

-

meiosis

fertilization

meiosis

fertilization

meiosis

fertilization

meiosis

fertilization

Sporophyte (diploid)

Chlorophyceae

Chlamydomonas reinhardtii

Charophyceae

Chara braunii

Liverwort

Marchantia polymorpha

Angiosperm

Arabidopsis thaliana