Chapter 17

Evolution of vascular plant body plans: a phylogenetic perspective

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ABSTRACT

Extant vascular plants comprise three major lineages: Lycophytina, Moniliformopses and Spermatophytata. We have investigated the evolution of body plans of vascular plants using a phylogenetic framework to reconstruct morphological character state changes. Our phylogenetic definition of body plans is based on synapomorphies of the lineages of extant vascular plants. Fundamental body plan features considered include the structure of meristems, the position of sporangia, spore/pollen wall development, and life cycle changes. Phylogenetic evidence supports the presence of roots in the common ancestor of extant vascular plants and a single origin of euphylls prior to the divergence of extant euphyllophytes. Heterochronic and heterotopic mutations and morphological simplification have each played major roles in the evolution of vascular plants. Phylogenetic evidence and the fossil record are integrated to reflect our current understanding of the evolution of vascular plants since their origin in the late Palaeozoic. The phylogenetic position of model organisms commonly used in developmental gene studies illustrates the importance of improving and diversifying taxon selection in future evolutionary studies that use developmental genes.

17.1 Introduction

Current studies in plant evolution focus on three themes: (1) phylogenetic relationships among extant and/or extinct lineages of vascular plants; (2) evolution of plant structures and shapes; and (3) the evolution of genes that control plant development. All of these themes are pertinent to what has become known as evolutionary developmental genetics. In the past, and to some extent still today, studies focusing on phylogenetic relationships and the evolution of form interpreted the anatomy and morphology of extant plant taxa using *ad hoc* statements to identify primitive or derived characters (Goebel, 1933; Bower, 1935; Troll, 1937, 1939; Campbell, 1940; Wardlaw, 1952, 1965; Kaplan, 1977; Kaplan and Groff, 1995; Kato and Imaichi, 1997; Hagemann, 1999; Niklas, 2000a, b). Several studies have also used the fossil record to reconstruct the first appearance of taxa and characters that were then used as empirical data to interpret plant relationships and the evolution of plant morphology (Zimmermann, 1959, 1965; Gensel, 1977, 1992; Gensel *et al.*, 2001). Investigations of developmental and functional aspects of plant structures, such as

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biomechanical properties in the reconstruction of fossils, have also been popular approaches to infer the evolution of vascular plants (Wardlaw, 1952, 1965; Speck and Rowe, 1999; Niklas, 2000a, b; DiMichele *et al.*, 2001).

Recently, two new approaches have made possible remarkable advancements in our understanding of plant evolution. In the first approach, plant phylogeny is inferred from the application of stringent analytical methods (e.g. maximum parsimony and maximum likelihood optimisation criteria) to both DNA sequence data and morphological data. These studies have allowed new insights into plant relationships (Donoghue and Doyle, 2000; Soltis and Soltis, 2000; Pryer *et al.*, 2001) and the interpretation of morphological character evolution (Crane and Kenrick, 1997; Kenrick and Crane, 1997; Bateman *et al.*, 1998; Doyle and Endress, 2000; Graham *et al.*, 2000; Renzaglia *et al.*, 2000). The second approach is based on the growing understanding of the role of dedicated genes (e.g. transcription factors) in controlling plant development, which has inspired new studies that focus on plant development in an evolutionary context (Doyle, 1994; Kramer and Irish, 1999, 2000; Frohlich and Parker, 2000; Lawton-Rauh *et al.*, 2000; Riechmann *et al.*, 2000; Vergara-Silva *et al.*, 2000). Varied terms have been used for the genetic factors involved in the regulation of plant development, such as receptors, transducers and transcription factors (Doebley and Lukens, 1998). Here, we use the term 'developmental genes' in a broad sense (Arthur, 1997; Gilbert, 2000; Morange, 2000). In plants, MADS-box genes are the most commonly studied developmental genes used to infer the evolution of key features of seed plants, such as the evolution of flowers (Hasebe, 1999; Hasebe and Ito, 1999; Shindo *et al.*, 1999; Winter *et al.*, 1999; Alvarez-Buylla *et al.*, 2000a, b; Becker *et al.*, 2000; Krogan and Ashton, 2000; Smyth, 2000; Svensson *et al.*, 2000; Theißen, 2000; Theißen *et al.*, 2000; Vergara-Silva *et al.*, 2000). Other kinds of plant developmental genes, such as homeodomain genes (Bharathan *et al.*, 1997, 1999; Aso *et al.*, 1999; Richards *et al.*, 2000; Sakakibara *et al.*, 2001), MYB genes (Kranz *et al.*, 2000) and phytochrome genes (Schneider-Poetsch *et al.*, 1998; Basu *et al.*, 2000), have been utilised in only a few evolutionary studies. Other studies have explored the evolution of actin genes, which encode a major component of the cytoskeleton, because duplication and modification of these genes is involved in the evolution of morphological complexity at the cellular level (Bhattacharya *et al.*, 2000).

The potential of these new sources of data to answer long-standing questions about plant evolution is staggering. Developmental genes, such as HOX-box genes, have already provided critical insights into the genetic basis of the developmental evolution of animals (Hall, 1996; Raff, 1996; Arthur, 1997; Gellon and McGinnis, 1998; Graham, 2000; Grbic, 2000; Jenner, 2000; Kappen, 2000; Peterson and Davidson, 2000; Wray and Lowe, 2000), prompting the application of similar approaches to plants (Hasebe, 1999; Kramer and Irish, 1999, 2000; Theißen, 2000; Vergara-Silva *et al.*, 2000). A future challenge will be to integrate phylogenetic reconstruction, morphological studies and developmental genetic data (Bateman, 1999; Valentine *et al.*, 1999; Kellogg, 2000a; Mabee, 2000). A series of nested studies might be envisaged to meet this challenge: (1) nucleotide sequence data of coding and/or non-coding DNA regions can be used to reconstruct the phylogeny; (2) extensive data sets comprising anatomical, biochemical, cytological and morphological characters can be used to infer character evolution on the resultant phylogeny; and (3) the phylogeny, with its explicit character transformation statements, can be compared to gene trees based on sequence data of developmental genes to further our understanding of the evolution of plant development. Researchers favouring a total evidence approach (de Queiroz, 2000; Hillis and Wiens, 2000) could combine steps 1 and 2 to construct a phylogeny based on both morphological and molecular data. Whatever the approach used, it seems advisable to maintain step 3 as an independent exercise.

A recent phylogenetic study by Pryer *et al.* (2001) utilising five data sets comprising three chloroplast genes (*atpB*, *rbcL*, *rps4*), nuclear small subunit (SSU) ribosomal DNA, and an extensive morphological matrix resulted in a new understanding of the relationships among major lineages of extant vascular plants. They refuted previous hypotheses of spore-bearing vascular plants as transitional evolutionary grades between bryophytes and seed plants. In particular, the hypothesis that *Psilotum* is a 'living fossil' with a close relationship to Lower Devonian psilophytes (Kaplan, 1977; Wagner, 1977; Rothwell, 1999) no longer appears tenable. These results call for a reinterpretation of the evolution of plant morphology. Reconstruction of phylogeny and morphological character state changes allows us to infer the relationship between ontogeny and phylogeny (Rieppel, 1993; Bang *et al.*, 2000; Collazo, 2000), mechanisms of evolution (Hall, 1996; Raff, 1996, 1999; Arthur, 1997, 2000a; Budd, 1999; Donoghue and Ree, 2000; Gibson and Wagner, 2000; Wagner and Schwenk, 2000), and the acquisition of 'key innovations' and body plans in the evolution of organisms (Arthur, 2000b; Graham *et al.*, 2000; Wagner *et al.*, 2000).

17.2 Methodology

17.2.1 Reconstruction of phylogenetic relationships

A phylogeny of vascular plants comprising representatives from all major extant clades was reconstructed using maximum likelihood analysis of nucleotide sequences from three chloroplast genes (*atpB*, *rbcL*, *rps4*) and nuclear SSU rDNA (Pryer *et al.*, 2001). This phylogeny is referred to subsequently as 'Phylogeny 2001'. Relationships among the bryophyte outgroups are the subject of current controversy (Lewis *et al.*, 1997; Nickrent *et al.*, 2000; Qiu and Lee, 2000). Because Phylogeny 2001 exhibited a polytomy among the outgroups, we follow here a most recent hypothesis of the relationships among the four lineages of land plants (Lewis *et al.*, 1997; Nickrent *et al.*, 2000; Qiu and Lee, 2000) in order to optimise character state reconstruction (Maddison and Maddison, 1992). Three alternative topologies, in which the sister group to tracheophytes is either (1) hornworts, (2) mosses or (3) a clade comprising liverworts and mosses, were considered initially. Reconstruction of character states within the vascular plants was not affected by these outgroup choices; therefore, character state changes were reconstructed using liverworts (Marchantiomorpha) as outgroup.

17.2.2 Reconstruction of character evolution

Characters taken from an extensive morphological data set were mapped onto Phylogeny 2001 (see Section 17.2.1). This morphological data set consists of 136 characters, including features of general morphology, anatomy, cytology, biochemistry and some structural DNA data. The data set was especially designed for an independent analysis of phylogenetic relationships among vascular plants and does not generally include characters that are of interest only for terminal groups such as flowering plants, horsetails, derived ferns, or for relationships among the outgroups. The morphological data matrix is available from the senior author. Character evolution was reconstructed for this data set using both accelerated transformation (Acctran) and delayed transformation (Deltran) optimisation as implemented in MacClade 3.0 (Maddison and Maddison, 1992). Character state changes were treated as ambiguous if the application of the two optimisation criteria resulted in different reconstructions. All characters shown in Figures 17.2–17.8 are treated as unordered. The reconstructed phylogeny (Section 17.3) and optimised character state changes (Section 17.4) formed the basis of an investigation into the nature of evolutionary transformations among vascular plants (Section 17.5).

17.3 Phylogeny of vascular plants (phylogenetic statements)

Extant vascular plants comprise three major lineages (Phylogeny 2001, Figure 17.1): lycophytes, seed plants and non-lycophyte pteridophytes. The third lineage comprises leptosporangiate ferns (Polypodiidae), two extant lineages of eusporangiate ferns (Marattiidae, Ophioglossidae), whisk ferns (Psilotidae) and horsetails (Equisetopsida). This clade is referred to throughout this chapter as Moniliformopses (or moniliforms), reflecting a classification first introduced by Kenrick and Crane (1997). The horsetails (Equisetopsida) and Marattiidae form a clade that is, in turn, sister to the leptosporangiate ferns (Polypodiidae). The basalmost branch of the Moniliformopses is a clade that includes Psilotidae and Ophioglossidae. Within seed plants, angiosperms are shown as sister to a monophyletic gymnosperm clade. This is not the first time that the anthophyte hypothesis has been refuted. Other phylogenetic analyses using DNA sequence data and denser taxonomic sampling also show that Gnetaceae is not sister to angiosperms (Doyle, 1996, 1998; Donoghue and Doyle, 2000; Sanderson *et al.*, 2000). Here, *Gnetum* is sister to the conifer *Pinus*; similar topologies are reported in recent studies focused on seed plant phylogeny (Doyle, 1998; Barkman *et al.*, 2000; Bowe *et al.*, 2000; Chaw *et al.*, 2000; Donoghue and Doyle, 2000).

17.4 Character evolution of vascular plants

17.4.1 Character state changes and vascular plant lineages

The total number of character state changes, as well as the number of unambiguous character state changes, are reported for each branch in Figure 17.1 for the 136 morphological characters that were mapped onto Phylogeny 2001. The morphological data set did not include characters that are informative only for terminal groups (e.g. floral characters). The number of character state changes, therefore, is relatively low for several derived branches.

The branches supporting the main lineages of vascular plants have relatively high

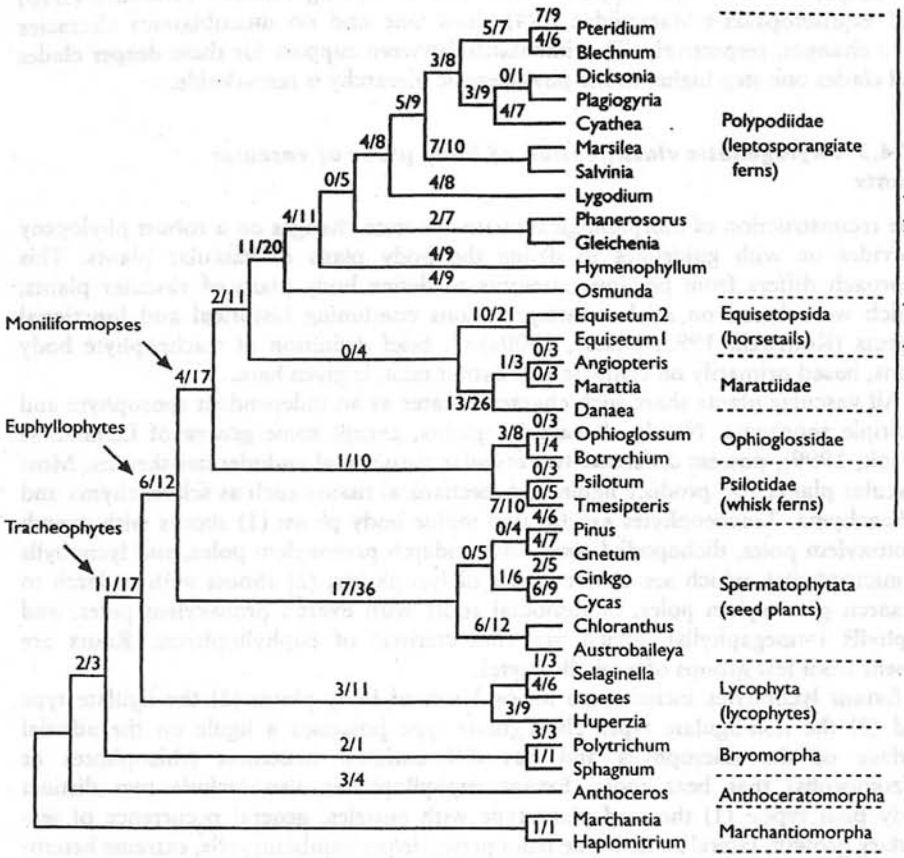

Figure 17.1 Phylogeny of vascular plants (referred to as Phylogeny 2001 throughout the text) as shown in Pryer *et al.* (2001), except for outgroup relationships, which have been redrawn (see Section 17.2.1). Character state evolution was reconstructed for 136 morphological characters using this phylogeny. The number of unambiguous morphological character state changes is given for each branch; total number of morphological character states changes (ambiguous + unambiguous) is shown after the slash. Taxonomy follows Kenrick and Crane (1997).

numbers of unambiguous and total character state changes: Lycophyta (3/11), Euphyllophytes (6/12), Spermatophytata (17/36), Moniliformopses (4/17) (Figure 17.1). The number of character state changes for the seed plant clade is high, reflecting the remarkable evolutionary transformation of major morphological features within this lineage after its divergence from other vascular plants. The majority of these spermatophyte character state changes are associated with the evolution of seeds. Within Moniliformopses, each of the five principal lineages shows a relatively high number of character state changes: Equisetopsida (10/21), Marattiidae (13/26), Ophioglossidae (3/8), Polypodiidae (11/20), Psilotidae (7/10). In striking contrast, the deeper branches that support clades such as Ophioglossidae + Psilotidae (1/10) and Equisetopsida + Marattiidae (0/4) show one and no unambiguous character state changes, respectively. This imbalance between support for these deeper clades and clades one step higher in the phylogenetic hierarchy is remarkable.

17.4.2 Phylogenetic classification of body plans of vascular plants

The reconstruction of morphological character state changes on a robust phylogeny provides us with guidelines to define the body plans of vascular plants. This approach differs from previous attempts to define body plans of vascular plants, which were based on *ad hoc* interpretations combining historical and functional aspects (Rothwell, 1995; Niklas, 2000a). A brief definition of tracheophyte body plans, based primarily on characters of extant taxa, is given here.

All vascular plants share such character states as an independent sporophyte and multiple sporangia. Nearly all vascular plants, except some genera of Lemnaceae (Cook, 1999), possess differentiated vascular tissues and endodermal sheaths. Most vascular plants also produce lignin and mechanical tissues such as sclerenchyma and collenchyma. Tracheophytes exhibit two major body plans: (1) shoots with exarch protoxylem poles, dichopodial roots with endarch protoxylem poles, and lycophylls (=microphylls), which are characteristic of lycophytes; (2) shoots with endarch to mesarch protoxylem poles, monopodial roots with exarch protoxylem poles, and euphylls (=megaphylls), which are characteristic of euphyllophytes. Roots are absent from few groups of euphyllophytes.

Extant lycophytes include two major kinds of body plans: (1) the ligulate type and (2) the non-ligulate type. The ligulate type possesses a ligule on the adaxial surface of the microphylls and has differentiated structures (rhizophores or rhizomorphs) that bear roots. Extant euphyllophytes also include two distinct body plan types: (1) the seed plant type with eusteles, general occurrence of secondary growth, lateral roots borne from pericycle/pericambium cells, extreme heterospory and seeds; and (2) the moniliform type with solenosteles (or dictyosteles), generally lacking secondary growth, lateral roots borne from endodermis cells, periplasmodial tapetum, pseudoendospore and spore wall development that is exclusively centrifugal.

Extant moniliforms include five main body plans that correspond to each of the main lineages: (1) the psilotoid-type is defined by the absence of roots, reduced euphylls, and differentiation of the shoot into an erect photosynthetic portion and a creeping non-photosynthetic portion; (2) the ophioglossoid-type is defined by a reduction in the number of euphylls to one per shoot produced at any given time, usually unbranched roots, and the absence of root hairs; (3) the marattioid-type is defined by shoots with polycyclic steles, roots with septate root hairs, and leaves with pulvini, scattered pneumathodes, and polycyclic vascular bundles; (4) the equisetoid-type is defined by reduced euphylls that are arranged in whorls, shoots differentiated into creeping and erect parts, presence of extensive lacunae systems in the ribbed shoots, and endogenous origin of lateral shoots; and (5) the polypodioid-type is defined by the occurrence of leptosporangiate sporangia formed from single epidermal cells, a reduced number of protoxylem poles per root (in general two), and the absence of a root pith.

Extant seed plants include two major body plans: (1) the gymnosperm-type with embryos that arise from a multinucleate zygote, phloem tissue with Strassburger cells, and secondary xylem cells of the coniferoid-type; and (2) the angiosperm-type with embryos that arise from a uninucleate zygote, phloem tissue with companion cells, a secondary endosperm, and flowers. Detailed definitions of the four body plan subtypes nested within the gymnosperm-type (cycadoid, ginkgoid, gnetoid, coniferoid) are not presented here because definitions need to be based on a phylogenetic analysis with a broader taxon sampling of seed plants.

17.4.3 Evolution of main features of vascular plants

The evolution of tracheophyte characters in comparison to other land plants and green algae has been examined in detail in previous studies (Kenrick and Crane, 1997; Edwards, 1999; Graham *et al.*, 2000; Renzaglia *et al.*, 2000). In the following text, we infer the evolution of a few selected characters (Figures 17.2–17.8) within vascular plants using Phylogeny 2001 (Pryer *et al.*, 2001).

A. Life cycle

Although the evolution of the life cycle of land plants has been explored in previous studies (Kenrick, 1994; Kenrick and Crane, 1997), differences in the life cycles among tracheophytes have yet to be examined in detail. It has been suggested that bryophytes and tracheophytes share a common ancestor possessing isomorphic gametophytic and sporophytic phases (Kenrick, 1994; Kenrick and Crane, 1997), whereas extant land plants have two phases that differ in form (heteromorphic) and duration. It is well known that vascular plants differ from bryophytes in having a dominant (or co-dominant) and independent sporophyte (Figure 17.2a, b). In general, tracheophytes have a gametophytic phase that is short-lived, although this is not the case in several basal lineages (Lycopodiales, Marattiidae, Ophioglossidae, Psilotidae). Nevertheless, it appears that the condition of having extremely short-lived gametophytes and long-lived sporophytes has evolved at least three times within vascular plants: heterosporous lycophytes (Isoëtales, Selaginellales), seed plants (Spermatophytata), and leptosporangiate ferns (Polypodiidae) (Figure 17.2a).

Another interesting aspect of the life cycle of land plants is the existence of a period of dormancy, which is intercalated between the sporophytic and gametophytic phases in bryophytes and pteridophytes (in the form of a haploid spore), but which occurs between the gametophytic and sporophytic phases in seed plants (in the form of a diploid embryo enclosed in a seed) (Figure 17.2b).

B. Meristems

Sporophytes of euphyllophytes possess at least three kinds of apical or marginal meristems that are involved in the formation of new organs: shoot meristems, root meristems, and leaf meristems. Intercalary meristems and cambia are ignored here because in general they are not involved in the formation of new organs. Fossil

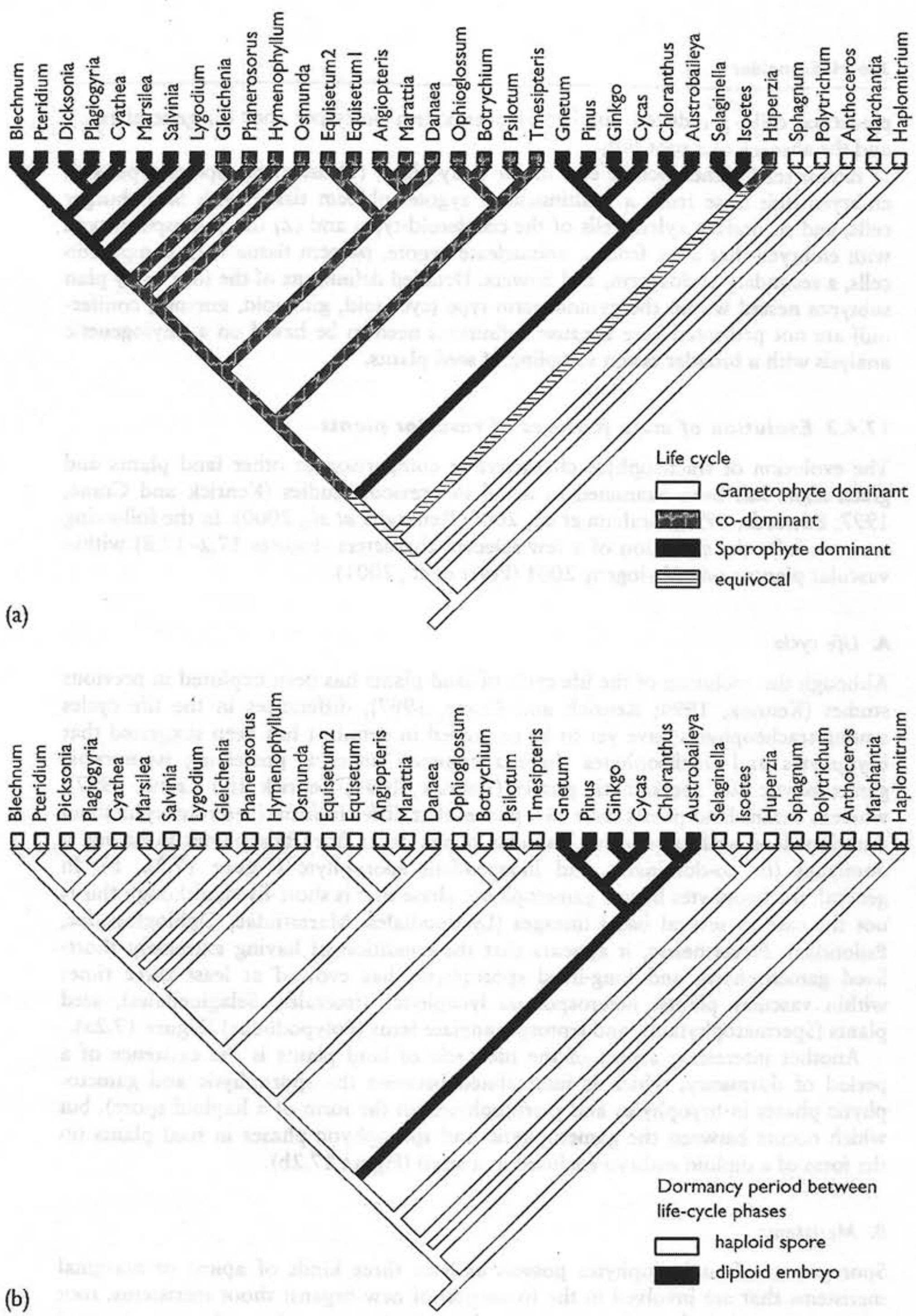

Figure 17.2 Life cycle features plotted on Phylogeny 2001. (a) Evolution of dominant life cycle phases in land plants. (b) Dormancy period between life cycle phases in land plants.

evidence suggests that the common ancestor of vascular plants possessed only one type of meristem per sporophyte and one type of meristem per gametophyte (Philipson, 1990; Kenrick and Crane, 1997). In bryophytes, the gametophytes possess only one meristem type, whereas the sporophytes have one apical shoot meristem or grow exclusively via an intercalary meristem (Kenrick and Crane, 1997).

Reconstruction of root evolution (Figure 17.3a) suggests a differentiation of shoot and root meristems in the common ancestor of all extant lineages of tracheophytes. Subsequent differentiation of meristem types in the common ancestor of the euphyllophytes resulted in a leaf meristem that produces euphylls (Figure 17.4b), whereas lycophylls grow exclusively with an intercalary meristem (Figure 17.4a). This scenario is consistent with the phylogeny but it needs to be confirmed with studies that address the genetic control of organogenesis and, in particular, organ identity. Genes controlling leaf identity of euphylls are assumed to be different from those controlling leaf identity of lycophylls (Kerstetter and Poethig, 1998; Foster and Veit, 2000; Frugis *et al.*, 1999; Tsukaya, 2000), whereas root identity genes are assumed to be homologous among tracheophytes (Benfey, 1999; Bai *et al.*, 2000; Costa and Dolan, 2000).

The three organs found in moniliforms (leaves, roots, shoots) have a meristem structure that has a single apical cell, similar to that found in bryophytes and the lycophyte lineage Selaginellales (Figure 17.5a). In contrast, the two other extant lineages of lycophytes (Lycopodiales and Isoëtales) and seed plants possess complex meristems. The meristems of lycophytes and seed plants differ substantially, and it is still unclear whether complex meristems are homologous, as proposed by Philipson (1990), or merely analogous.

C. Root–shoot differentiation

The root is one of the three basic organs of vascular plants, yet the phylogenetic origin of roots is rarely discussed (Zimmermann, 1965; Kutschera and Sobotik, 1997; Gensel *et al.*, 2001; Raven and Edwards, 2001). Some authors (Goebel, 1933; Hagemann, 1992, 1997, 1999) suggest that roots originated as tuberous storage organs. However, some Lower Devonian vascular plant fossils suggest that roots evolved from creeping, elongate shoot-like structures (Remy *et al.*, 1997; Gensel *et al.*, 2001; Raven and Edwards, 2001). It has been argued that roots of lycophytes and euphyllophytes are not homologous because roots are unknown from many Lower Devonian trimerophytes and zosterophytes (Gensel, 1992; Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Gensel *et al.*, 2001; Raven and Edwards, 2001). However, fossil evidence for roots is often ambiguous (Kenrick and Crane, 1997; Gensel *et al.*, 2001; Raven and Edwards, 2001) and root-like structures are known for some Lower Devonian taxa (Remy *et al.*, 1997; Gensel *et al.*, 2001; Raven and Edwards, 2001). Phylogenetic evidence indicates that roots of lycophytes and euphyllophytes are homologous (Figure 17.3a).

Roots of euphyllophytes and lycophytes share several structural features such as a calyptra, endogenous origin of the shoot-borne root and presence of root hairs, but they differ in two notable characters. First, shoot-borne roots of lycophytes show dichopodial branching, whereas shoot-borne roots of euphyllophytes show monopodial branching with lateral roots differentiated endogenously (Figure 17.3b). This

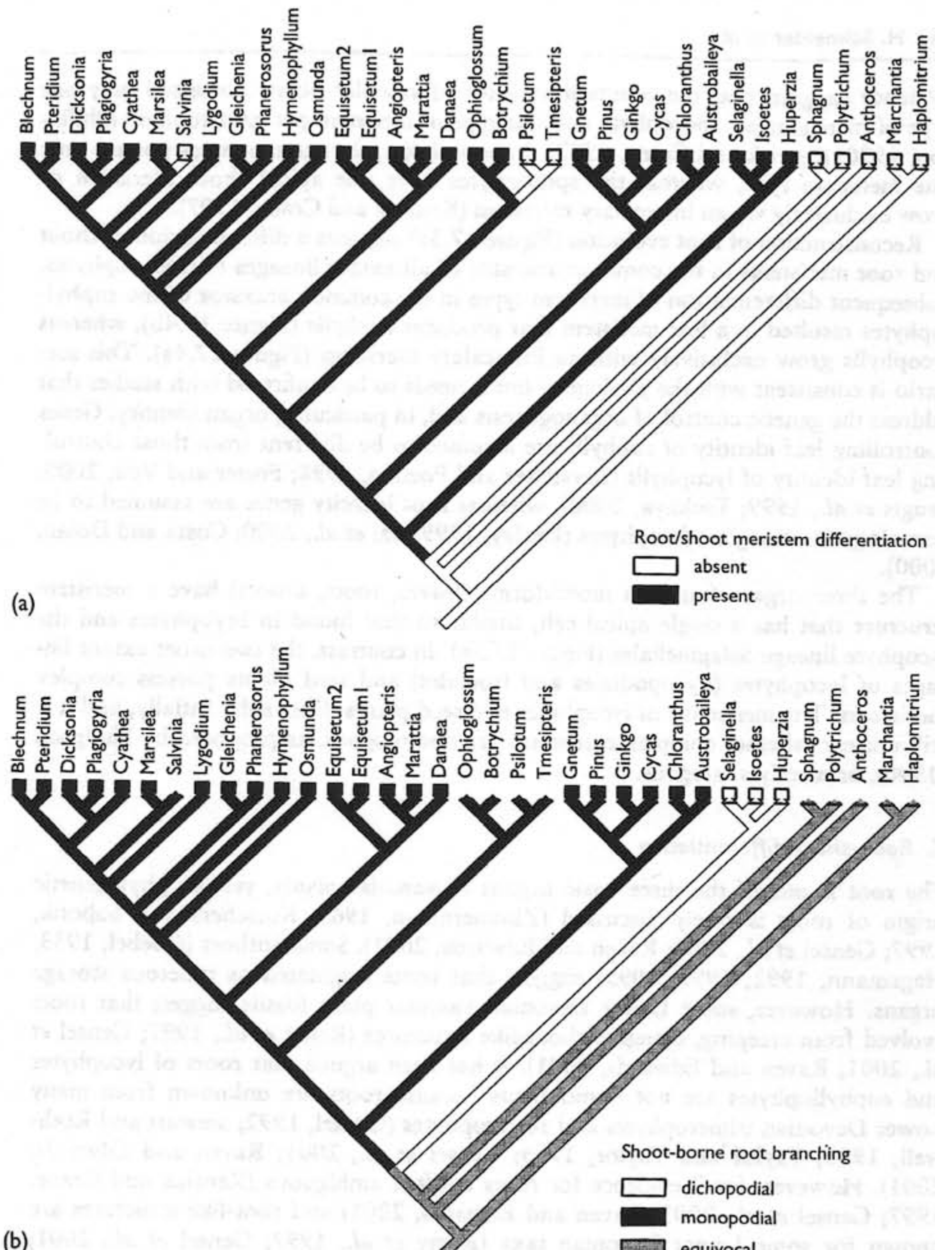

Figure 17.3 Root characters plotted on Phylogeny 2001. (a) Root/shoot meristem differentiation. (b) Branching of shoot-borne roots. The latter character is not applicable to taxa with unbranched shoot-borne roots (*Ophioglossum*, *Botrychium*) and rootless taxa such as bryophytes, whisk ferns (*Psilotum*, *Tmesipteris*) and *Salvinia*. Shoot-borne roots of *Ophioglossum* are unbranched, with the exception of *Ophioglossum palmatum*, which sometimes has dichotomously branched roots.

Figure 17.4 Leaf types plotted on Phylogeny 2001. (a) Lycophylls = lacking leaf gaps and an apical/marginal leaf meristem. (b) Euphylls = possessing leaf gaps and an apical/marginal leaf meristem.

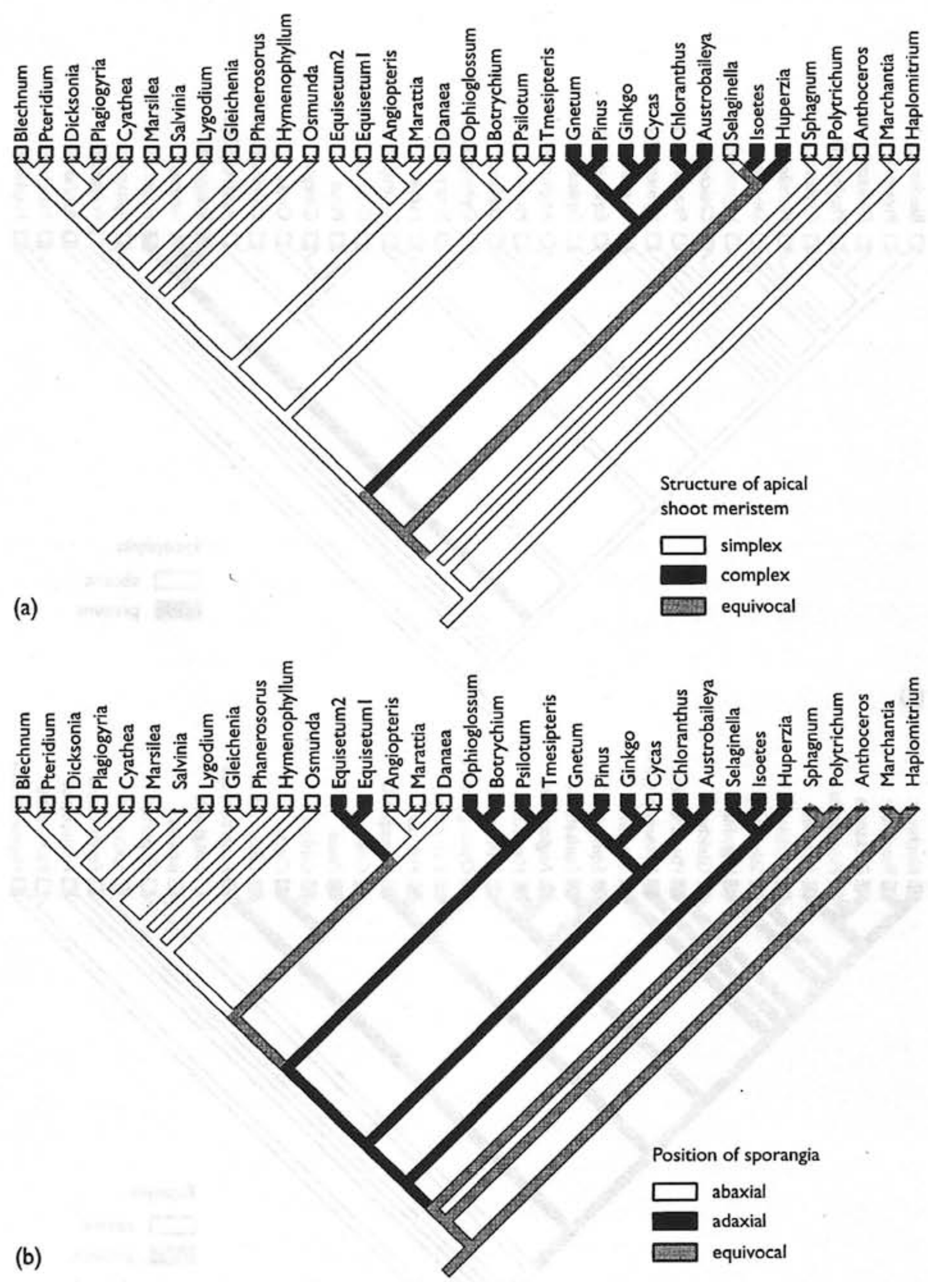

Figure 17.5 Shoot apical meristem structure and sporangial position plotted on Phylogeny 2001. (a) Shoot apical meristem organisation; simplex (with single apical cell) and complex (without a single apical cell), definitions according to Philipson (1990). (b) Position of sporangia relative to leaf-like organs; adaxial sporangia are attached to the shoot above the leaf or on the adaxial surface of the leaf, abaxial sporangia are attached to the abaxial surface of the leaf. *Salvinia* is scored as unknown because the interpretation of the highly modified, submerged, sporangia-bearing organ is unclear. Seed plants are scored according to Doyle (1996). Bryophyte sporophytes lack leaf-like structures and the character is therefore not applicable.

character is not applicable to rootless taxa such as Psilotidae and taxa with unbranched roots, such as the majority of Ophioglossidae. Second, protoxylem poles are located in an endarch position in lycophytes but exarch in euphyllophytes. This character has a reverse correlation with the position of protoxylem strands in the shoot stele, which are exarch in lycophytes and endarch or mesarch in euphyllophytes.

The main features of roots are conserved in the evolution of euphyllophytes except in the Ophioglossideae + Psilotidae clade, where root systems are reduced or absent (Figure 17.3a, b). Leptosporangiate ferns (Polypodiidae) are characterised by the absence of a root pith. This loss of a root pith may have occurred twice in closely related lineages, Polypodiidae and Equisetopsida, or it may be a synapomorphy of the clade including these two lineages and Marattiidae, with a reversal in Marattiidae.

Several other characters of root systems correlate with characters found in other organs; for example, roots with secondary growth are found only in taxa with secondary shoot growth, and homorhizy is correlated with the presence of seeds.

D. *Leaf–shoot differentiation*

The evolution of leaves is often discussed with reference to various 'leaf' characters, such as dorsiventral organisation, leaf gaps, and branched venation (Arber, 1950; Wagner, 1977; Wagner *et al.*, 1982, Rutishauser, 1999; Dengler and Tsukaya, 2001). Recent phylogenetic studies support the independent origin of two leaf-like organs in vascular plants (Figure 17.4a, b): the lycophylls (=microphylls) of lycophytes, and the euphylls (=megaphylls) of euphyllophytes (Kenrick and Crane, 1997; Pryer *et al.*, 2001). Crane and Kenrick (1997) proposed that lycophylls are transformed sporangia, whereas euphylls appear to be modified shoot systems (Zimmermann, 1959, 1965). Differences of opinion surrounding leaf origin in land plants (Niklas, 2000a, b) can be attributed, in part, to the use of different criteria to define leaves (Rutishauser, 1999). Only two features are consistently present in all leaves of euphyllophytes (with very few exceptions) but always absent from lycophytes: leaf gaps and development by an apical or marginal meristem. A further observation is the association of euphylls with lateral branches (Arber, 1950; Rutishauser, 1999), which are always axial only in extant seed plants. In moniliforms, lateral branches are generally located close to, but rarely within, the axils of leaves (Galtier, 1999). In addition, shoot branching patterns were more varied in Palaeozoic seed plants than they are in extant ones, and included non-axial and axial lateral branches (Galtier, 1999).

Other features used to define leaves often reflect functional specialisation and therefore are not useful for determining homology. For example, leaf-like structures of bryophytes and vascular plants share a planar shape, yet this is not an indicator of homology but is probably the result of functional constraints (Beerling *et al.*, 2001; Raven and Edwards, 2001). Branched veins in leaves of a few species of *Selaginella* (Wagner *et al.*, 1982) are also likely to be the result of independent evolutionary innovation and not evidence for their homology with euphyllophyte leaves. Similarly, several leaf characters, such as dorsiventral organisation, petiole-blade differentiation, marginal meristem, simple blades, anastomosing venation, and differentiation of palisade and spongy parenchyma, may have evolved or been lost independently in different lineages after the establishment of euphylls.

The homology of leaves of ferns and seed plants has been questioned (Wagner *et al.*, 1982; Rutishauser, 1999) even though they share the occurrence of leaf gaps and of apical and/or marginal meristems. Leaves of extant members of these lineages do differ substantially in their development (Hagemann, 1984), but similar foliage patterns observed in progymnosperms and ferns suggest that a shared developmental program of leaf formation existed in the common ancestor of moniliforms and seed plants. Angiosperms have a notable diversity of leaf development patterns (Tsukaya, 2000; Kaplan, 2001), but a comparative study including other seed plant lineages is lacking. Some features such as basipetal growth (Hagemann, 1984; Tsukaya, 2000) are likely to be restricted to flowering plants.

Current studies of genes that control leaf identity and formation have been carried out exclusively on derived angiosperms (Bowman, 2000; Foster and Veit, 2000; Tsukaya, 2000; Dengler and Tsukaya, 2001), and the results were rarely reported in a comparative framework and, unfortunately, never with a phylogenetic perspective. The remarkable diversity of leaf shapes and structures in early euphyllophytes (Taylor and Taylor, 1993; Galtier and Phillips, 1996) is evident in some features of the leaves of horsetails (Equisetopsida), whisk ferns (Psilotidae) and moonworts (Ophioglossidae). In horsetails and whisk ferns the leaves are extremely reduced and no leaf gap is present in *Psilotum*. However, the closely related genus *Tmesipteris* possesses larger leaves with leaf gaps. The leaves of Psilotidae and Ophioglossidae are not associated with lateral branches but with fertile structures called sporangiophores. The homology of these structures is unclear, but it is thought that they are reduced branches. In addition, the long and extensive fossil record of members of the horsetail lineage documents a reduction (simplification) of the leaves during their evolution (Zimmermann, 1965; Stewart and Rothwell, 1993; Taylor and Taylor, 1993).

E. Position of sporangia

Sporangia are found attached either to the adaxial or abaxial surface of a leaf-like structure (Figure 17.5b). Abaxial sporangia are found in Polypodiidae and Marattiidae, whereas adaxial sporangia are found in the most basal lineage of moniliforms comprising Ophioglossidae and Psilotidae. Traditional interpretations of the position of sporangia in Equisetopsida (Stewart and Rothwell, 1993; Taylor and Taylor, 1993) suggest an attachment of the sporangia to an adaxial sporangiophore, similar to the condition found in Psilotidae and Ophioglossidae. This hypothesis indicates either an independent origin of abaxial sporangia in Marattiidae and Polypodiidae or a reversal to the adaxial position in Equisetopsida (Figure 17.5b). According to Doyle (1996), most extant seed plants bear sporangia in an adaxial position.

F. Spore/pollen wall evolution

Spore and pollen wall formation is a highly conserved character within the major lineages of land plants. The exine of bryophytes, lycophytes and seed plants develops in two directions, centripetally and centrifugally, but the exine of moniliforms develops exclusively centrifugally (Figure 17.6a) (Rowley, 1996). Moniliforms share several unique features of spore development and structure, such as periplasmodial

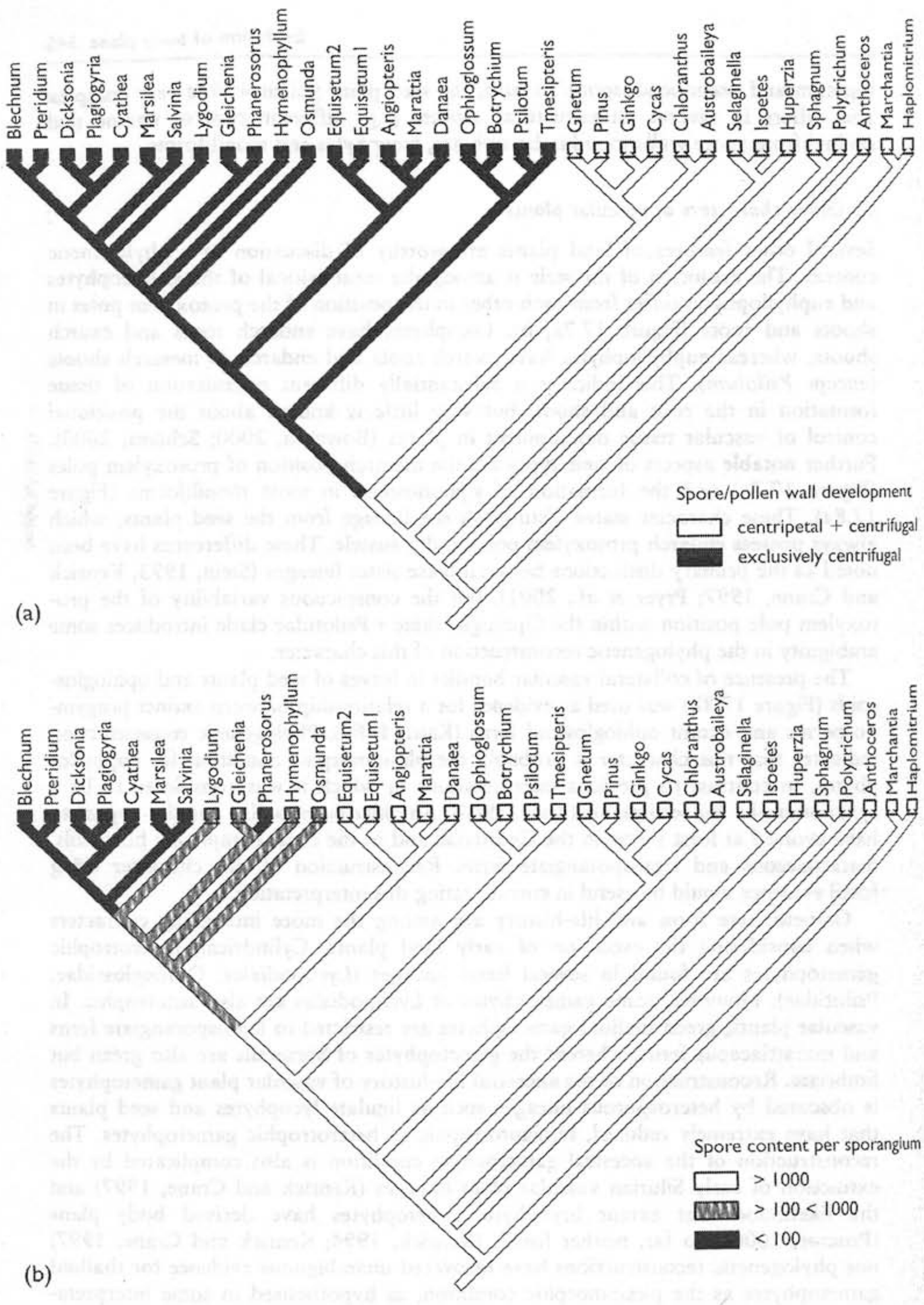

Figure 17.6 Spore characters plotted on Phylogeny 2001. (a) Spore/pollen wall develops in two directions, centripetally (inwardly) and centrifugally (outwardly), or in only one direction (centrifugally). (b) Spore content per sporangium.

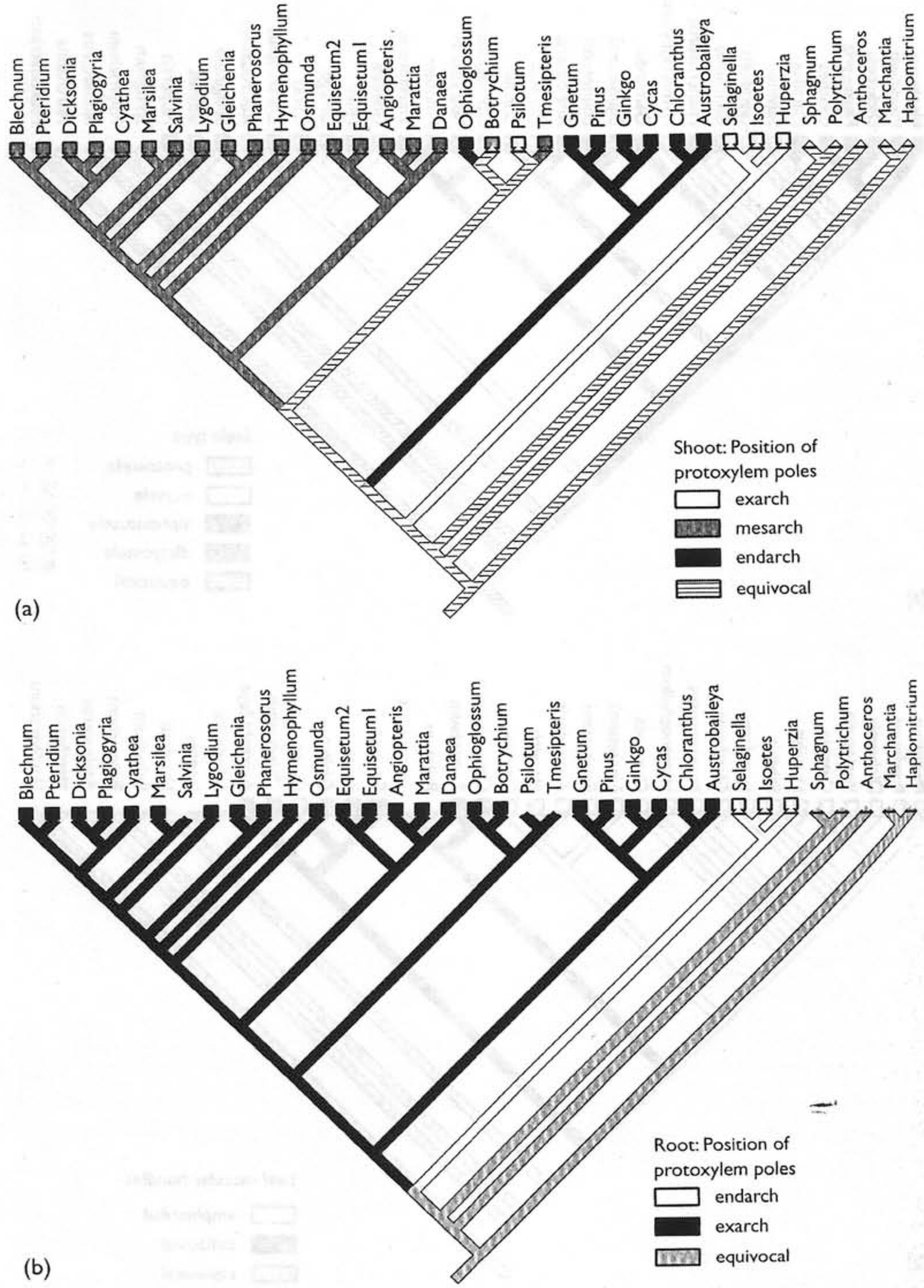

Figure 17.7 Vascular tissue characters plotted on Phylogeny 2001. (a) Position of protoxylem poles in shoot stele. (b) Position of protoxylem poles in root vascular bundle. The latter character is not applicable to rootless taxa such as *Salvinia* and Psilotaceae. Neither character is applicable to bryophytes.

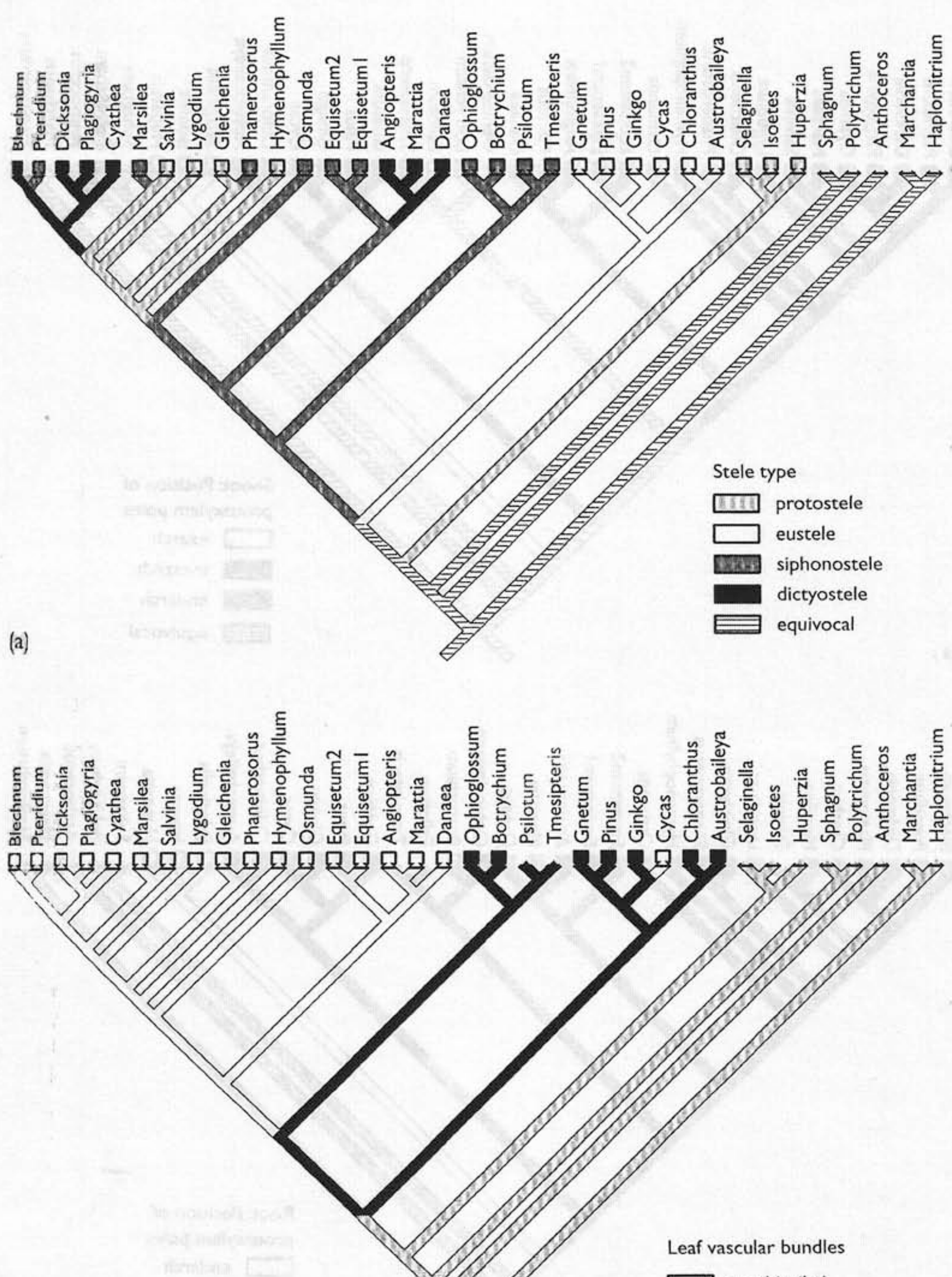

Figure 17.8 Vascular tissue characters plotted on Phylogeny 2001. (a) Structure of the stele in the mature shoot. (b) Structure of the vascular bundles in the leaf. Vascular tissue in leaves of Psilotidae is highly reduced and is scored as an unknown character state. Neither character is applicable to bryophytes.

fossils have suggested that early land plant gametophytes were cylindrical (Gensel, 1992; Kenrick, 1994; Kenrick and Crane, 1997; Edwards, 1999; Gensel *et al.*, 2001).

17.5 Categories of transformations involved in the evolution of vascular plants

17.5.1 Iteration

Plants are modular organisms and in general each structure exists in several multiplications (Tomlinson, 1984). It is, therefore, difficult to identify duplication events of phylogenetic significance. Nevertheless, one example is the multiplication of vascular stele cycles resulting in polycyclic structures within shoots or petioles. Polycyclic steles are rare, occurring in only a few lineages of moniliforms, but they characterise the Marattiidae. A further example of multiplication without modification is the increased number of sperm cell flagellae in euphyllophytes (Renzaglia *et al.*, 2000).

17.5.2 Modification of plant development

A. Heterochrony

Several character state changes may be caused by heterochronic mutations that result in an alteration in the sequence and timing of developmental processes (Mosbrugger, 1995; Raff, 1996; Friedman and Carmichael, 1998; Klingenberg, 1998; Gould, 2000; Kellogg, 2000a; Li and Johnson, 2000). Changes in the length of the gametophytic or sporophytic phases, as discussed above in Section 17.4.3A, are likely to be the result of heterochronic events in the evolution of vascular plants (Figure 17.2a). For example, extremely short-lived gametophytes have arisen at least three times: ligulate lycophytes, seed plants and heterosporous leptosporangiate ferns. Another possible example of heterochrony is the shift of the dormancy period between life phases from the haploid spore to the diploid embryo enclosed in the seed (Figure 17.2b). This transformation is correlated with the evolution of seeds, and recent studies of the evolution of seed storage globulins have demonstrated that a vicilin-like protein is specifically expressed in fern spores (Shutov *et al.*, 1998). In seed plants, members of this gene family are expressed exclusively in the seed (dormancy phase). Heterochronic transformations may also be responsible for the reduction in number of spores produced per sporangium (Section 17.5.3; Figure 17.6b).

B. Heterotopy

Several character state changes may be caused by heterotopic mutations that result in relocation of structures in the evolution of vascular plant body plans (Sattler, 1988, 1994; Sattler and Rutishauser, 1997; Kellogg, 2000a). Examples of heterotopic mutations are observed in anatomical characters, such as in the position of protoxylem poles or sclerenchymatous tissue. As discussed in Section 17.4.3G, the position of protoxylem poles in the root and the shoot is an important distinction between lycophytes and euphyllophytes (Figure 17.7a, b). The endarch or mesarch position of protoxylem in the shoot distinguishes the seed plants and moniliforms except for the Ophioglossidae + Psilotidae clade, which is distinct from all other vascular plant lineages in having taxa with endarch, exarch or mesarch protoxylem poles. Notably, it includes *Psilotum*, the only extant euphyllophyte with exarch protoxylem poles in the shoot stele, a character state otherwise restricted to lycophytes, whereas its sister genus *Tmesipteris* has mesarch protoxylem poles, which are typical of moniliforms. Phylogenetic changes in the localisation of tissues such as protoxylem are likely due to changes in the positional control of cell differentiation (Benfey, 1999; Dolan and Okada, 1999; Costa and Dolan, 2000). Sclerenchymatous tissue in the root cortex of leptosporangiate ferns (Polypodiidae) exemplifies relocation of cell types (Schneider, unpubl. obs.). Sclerenchymatous cells, if present, are differentiated either in the inner or the outer cortex. Sporangial position is also an example of structural relocation in the evolution of vascular plants (Figure 17.5b). The sporangia in moniliforms are located either on the abaxial side of the leaves or adaxially on sporangiophores (Section 17.4.3E). The phylogeny indicates one or perhaps two transitions of sporangia from an adaxial to abaxial position in moniliforms (Figure 17.5b).

C. Heterometry

Little evidence for heterometric mutations that result in changes in size of structures (Zelditch and Fink, 1996; Gould, 2000) was found with this data set because quantitative characters were excluded. They are of great interest in studies of the evolution of closely related species but less informative for studies of deep phylogenies.

17.5.3 Simplification is ubiquitous in plant evolution

Duplication and subsequent modification result in a general trend towards increasing the complexity of body plans of vascular plants (Valentine, 2000), but several derived lineages are characterised by the reduction or absence of structures (Bateman, 1996; Pryer *et al.*, 2001). Obvious examples of simplification are the deletion of organs during evolution. Psilotidae are rootless, but phylogenetic reconstructions indicate that their ancestors possessed roots (Figure 17.3a). Rootless plants are found also in other clades of vascular plants, such as the heterosporous fern *Salvinia* (Polypodiidae) and in flowering plants (e.g. *Ceratophyllum*, *Wolffia*). The absence of lateral roots and root hairs in the Ophioglossidae, the sister clade of Psilotidae, indicates that reduction of the root system is a shared trait of the Ophioglossidae + Psilotidae clade (Figure 17.3b), in which roots are either completely absent (Psilotidae) or develop only as unbranched, shoot-borne roots without root hairs (Ophioglossidae).

Other simplifications include the absence of mechanical tissue (collenchyma and sclerenchyma) in Ophioglossidae and some Marattiidae, the reduction of euphylls to scale-like structures in Psilotidae and Equisetopsida, and the absence of a root pith in all Polypodiidae. The reduction in spore wall thickness and the number of spores produced per sporangium in leptosporangiate ferns (Polypodiidae) are both examples of simplification that may be explained by heterochronic or heterometric mutations. The relatively gradual reduction in spore number per sporangium in leptosporangiate ferns is particularly notable (Figure 17.6b), proceeding sequentially from more than 1000, to less than 1000 but more than 100, and finally to less than 100 (usually exactly 64). Heterochronic mutations may also be responsible for the reduction observed in leaf production in Ophioglossidae; only a single leaf is produced each growing season.

17.6 Implications of a phylogeny for current studies

17.6.1 Time-scale and the evolution of vascular plant lineages

It is now generally accepted that the age of a given lineage of organisms can be inferred from a combination of phylogenetic reconstruction and dates of first appearance of the lineage in the fossil record (Norell and Novacek, 1992; Wagner, 1995; Kenrick and Crane, 1997). Data regarding first appearances of various vascular plant lineages are available in several recent studies (Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Collinson, 1996; Kenrick and Crane, 1997; Crane, 1999; Miller, 1999; Liu *et al.*, 2000). This approach for dating lineages is limited by gaps in the fossil record and is dependent on differentiating and correctly identifying the relationships among early Palaeozoic tracheophytes (Gensel, 1992; Galtier and Philips, 1996; Miller, 1999; Berry and Stein, 2000; Liu *et al.*, 2000; Berry and Fairon-Demaret, 2001; Gensel *et al.*, 2001). As a general rule, phylogenetic evidence provides age estimates that considerably pre-date first appearances in the fossil record. Psilotidae and Ophioglossidae are among the most prominent examples (Figure 17.9). Both are known only from Cenozoic fossils (Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Kenrick and Crane, 1997), whereas their phylogenetic placement necessitates an origin of the Ophioglossidae + Psilotidae clade no later than the Devonian. A similar conflict between phylogenetic topology and the fossil record exists among the seed plants, especially with regard to the origin of flowering plants (=Magnolidra). However, estimates for the age of the seed plant lineages based on DNA nucleotide sequences appear to be consistent with the topology in Figure 17.9 (Goremykin *et al.*, 1997; Magallón *et al.*, 2000). Further aspects of the phylogeny and fossil record were reviewed recently for Coniferidra (Miller, 1999), Marattiidae (Liu *et al.*, 2000) and Polypodiidae (Collinson, 1996; Schneider and Kenrick, 2001). With regard to reconstructing the evolution of plant development, it is important to note that the phylogeny (Figure 17.9) suggests that the major lineages of vascular plants, namely lycophytes, moniliforms and seed plants, have been evolving independently since the Devonian. In addition, extant representatives or close relatives of members of these three major lineages can be traced to a time before the Upper Devonian (lycophytes and moniliforms) or the Permian (seed plants). Such long separation times between the three major lineages may cause problems in studies attempting to infer the evolution of developmental genes (Becker *et al.*, 2000).

17.6.2 Model organisms reconsidered in a phylogenetic framework

A full understanding of the diversity and complexity of organisms is one of the major challenges in biology. Complex structures, such as genomes, can presently be

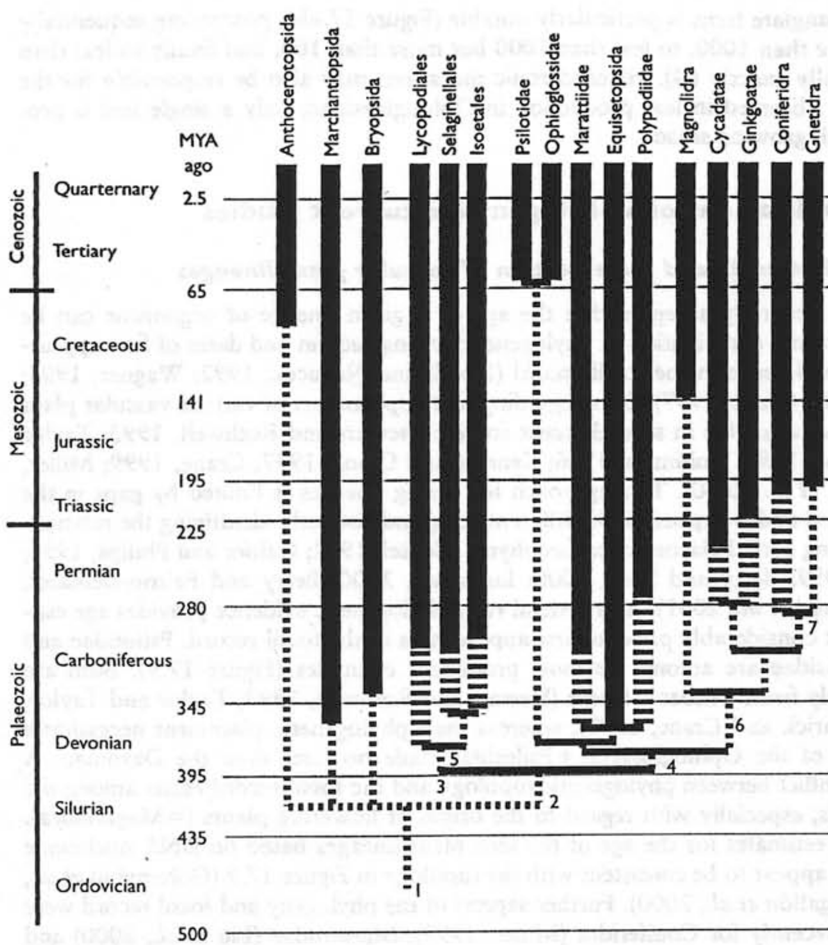

Figure 17.9 Estimate of the age of major lineages of land plants based on stratigraphic evidence (Stewart and Rothwell, 1993; Taylor and Taylor, 1993; Collinson, 1996; Kenrick and Crane, 1997; Doyle, 1998; Miller, 1999; Liu *et al.*, 2000) plotted on our best estimate of land plant phylogeny. Thick continuous lines indicate a fossil record for an extant lineage, thick dashed lines indicate a fossil record for close relatives of extant lineages (such as early conifers), thin dashed vertical lines indicate branches of ambiguous length caused by a conflict between the fossil record and phylogenetic evidence. Numbers indicate first fossil appearances used as calibration points: (1) first land plants, (2) first tracheophytes, (3) first lycophytes, (4) first Moniliformopses (e.g. *Ibyka*) and Radiatopses (e.g. *Crossia*), (5) first ligulate lycophytes (e.g. *Leclerqia*), (6) first seed plants (e.g. *Elkinsia*), (7) first conifers. The Ophioglossidae + Psilotidae clade is known only since the Tertiary; the age of the split between both lineages is ambiguous. The taxonomic classification is based on Kenrick and Crane (1997).

studied in detail only for a few species due to enormous cost considerations. Consequently, current scientific progress relies on the assumption that similar structures and processes are identical in various and often distantly related organisms, and plant developmental genetics focuses on only a few plant species as model organisms. To evaluate the current selection of plant model organisms used in developmental genetic studies, we identified their position in Phylogeny 2001 (Figure 17.1) and in more detailed phylogenetic studies for ferns (Hasebe *et al.*, 1995; Pryer *et al.*, 1995), flowering plants (Qiu *et al.*, 1999; Soltis *et al.*, 1999) and mosses (Goffinet and Cox, 2000). The phylogenetic positions of those model organisms for which developmental gene sequences have been reported are indicated in Figure 17.10.

The vast majority of plant model organisms are members of the more recently evolved lineages of angiosperms (Mandoli and Olmstead, 2000), and many of these are of noted economic importance, such as monocotyledons (Poaceae: *Zea*, *Oryza*, *Triticum*) and eudicots (Brassicaceae: *Arabidopsis*, *Brassica*; Scrophulariaceae: *Antirrhinum*; Solanaceae: *Lycopersicon* (=*Solanum*), *Nicotiana*, *Petunia*). A few studies have attempted to establish some gymnosperms (e.g. *Gnetum*, and the conifers *Picea* and *Pinus*) as additional model organisms, although their long generation times limit their usefulness for genetic studies (Lev-Yada and Sederoff, 2000). The fern *Ceratopteris* (Pteridacae, Polypodiidae) and the moss *Physcomitrella patens* (Funariaceae, Bryomorpha) have been widely used to represent pteridophytes and bryophytes, respectively (Chatterjee and Roux, 2000; Cove, 2000). All model organisms are members of the crown groups of their lineages, and most exhibit derived rather than ancestral features in their clade. In angiosperms, the herbaceous growth form typical of all model organisms is the derived condition (Qiu *et al.*, 1999; Soltis *et al.*, 1999; Doyle and Endress, 2000), and the fern *Ceratopteris* has an unusually rapid reproductive cycle (Hickok *et al.*, 1995; Banks, 1999; Chatterjee and Roux, 2000), which may indicate a fundamental modification in its reproductive biology from other leptosporangiate ferns. The reproductive biology of *Ceratopteris* is unlikely to be representative of the common ancestor of moniliforms and seed plants.

Several recent studies have inferred the evolution of various genes that were demonstrated to control the development of various plant structures (Riechmann *et al.*, 2000; Riechmann and Ratcliffe, 2000). These studies often include a broad taxon sample, but several critical taxa are usually lacking. MADS-box gene evolution is the best studied among these examples. These studies usually focus on seed plants (Hasebe, 1999; Shindo *et al.*, 1999; Winter *et al.*, 1999; Alvarez-Buylla *et al.*, 2000a, b; Becker *et al.*, 2000; Theißen *et al.*, 2000, 2002). *Ceratopteris*, and sometimes *Ophioglossum*, are included in some of these studies as the only non-seed plant representatives. Only recently have MADS-box genes been described for some other critical taxa, including the bryophyte *Physcomitrella patens* (Krogan and Ashton, 2000) and the lycophyte *Lycopodium annotinum* (Svensson *et al.*, 2000). The last two taxa have not yet been included in a phylogenetic study of MADS-box genes (but see Langdale *et al.*, 2002). In contrast, the sampling of seed plants for MADS-box genes has been much improved during the last few years, with sequences from Gnetatae (*Gnetum*), Coniferidra (*Picea*, *Pinus*), Ginkgoatae (*Ginkgo*) and Magnolidra (e.g. *Arabidopsis*, *Brassica*, *Oryza*, *Petunia*, *Solanum*) now available, although Cycadatae and representatives of basal lineages of angiosperms are still lacking.

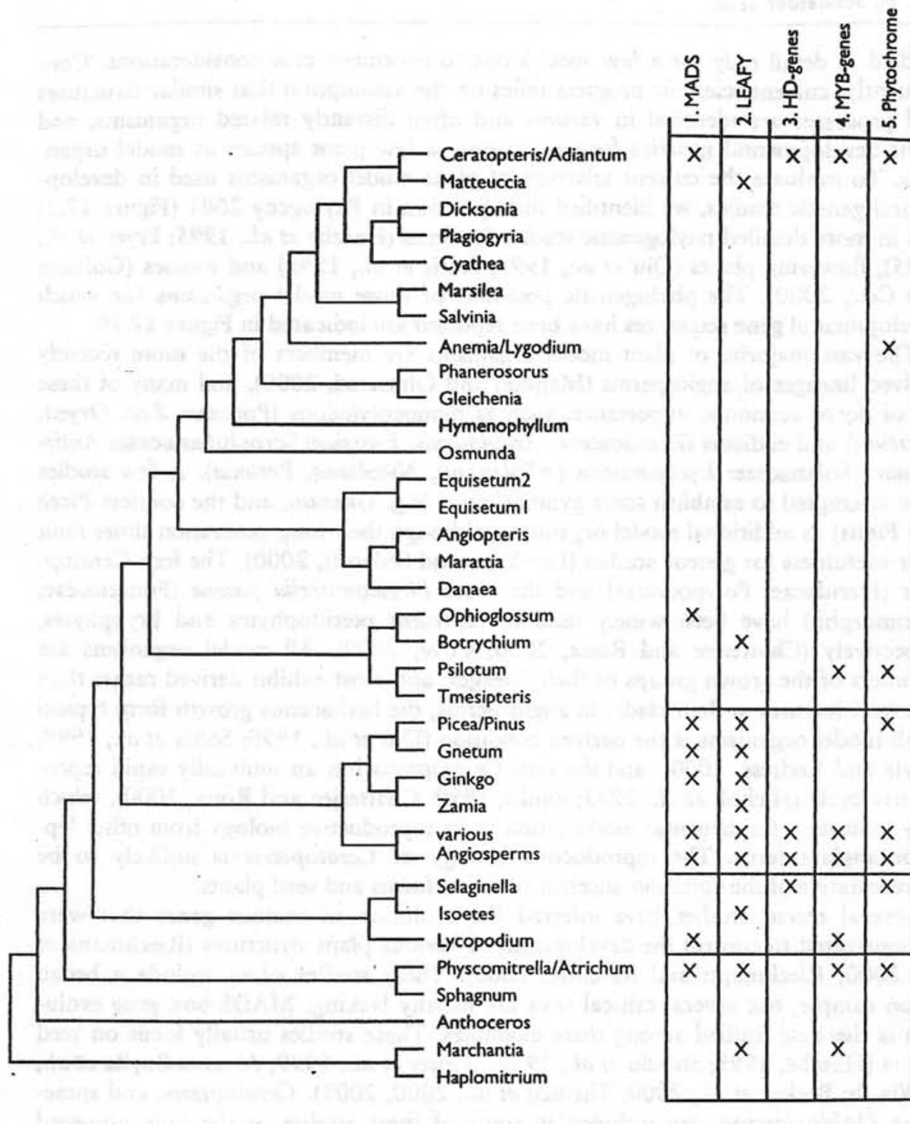

Figure 17.10 **Phylogenetic position of taxa with reported sequence data for five developmental gene families. (1) MADS-box (Winter *et al.*, 1999; Becker *et al.*, 2000; Krogan and Ashton, 2000; Svensson *et al.*, 2000; Theißen, 2000; Theißen *et al.*, 2002), (2) *LEAFY* (Frohlich and Estabrook, 2000; Frohlich and Parker, 2000; Frohlich, 2002), (3) HD-genes (Bharathan *et al.*, 1997, 1999; Juarez and Banks, 1997; Aso *et al.*, 1999; Reiser *et al.*, 2000; Champagne and Ashton, 2001; Sakakibara *et al.*, 2001), (4) *MYB* genes (Kranz *et al.*, 2000), (5) Phytochrome genes (Schneider-Poetsch *et al.*, 1998; Basu *et al.*, 2000). Not all of the sequences available for MADS-box, *LEAFY*, HD-genes and *MYB*-genes have been included in single comprehensive studies. Unfortunately, some sequences are not accessible because they have not been submitted to public gene databases.**

The phylogeny of another developmental gene, *LEAFY*, was inferred in recent studies including representatives of all five main lineages of seed plants and *Nymphaea* as representative of the basal lineage of angiosperms, but only two non-seed vascular plants were included (Frohlich and Estabrook, 2000; Frohlich and Parker, 2000; Frohlich, 2002). A third group of developmental genes, homeodomain proteins (HD genes), has been studied in the broad context of the evolution of this gene family in a clade including animals, fungi and plants (Bharathan *et al.*, 1997), but in plants they are known nearly exclusively from angiosperms. This is especially the case with one class of HD genes, the *KNOTTED* genes (Bharathan *et al.*, 1999). Although *KNOTTED* genes have been reported from the fern *Ceratopteris* (Juarez and Banks, 1997; Banks, 1999; Reiser *et al.*, 2000) and the bryophyte *Physcomitrella* (Champagne and Ashton, 2001), they have not been included in an extensive phylogenetic study. Several copies of homeodomain-leucine-zip genes (HD-zip genes) are known from the fern *Ceratopteris* and the bryophyte *Physcomitrella*, and have been included in a comprehensive phylogenetic analysis together with derived angiosperms (e.g. *Arabidopsis*, *Daucus*, *Oryza*) (Aso *et al.*, 1999; Sakakibara *et al.*, 2001). Other developmental genes, such as the *MYB* genes (Kranz *et al.*, 2000; Langdale *et al.*, 2002) and phytochromes (Schneider-Poetsch *et al.*, 1998; Basu *et al.*, 2000) have been studied with a better taxon sampling of bryophytes and pteridophytes than in MADS-box gene studies. For several developmental gene families, such as *YABBY* genes, which are involved in the control mechanisms of axial patterning (Bowman, 2000), no homologous sequences are known from bryophytes or pteridophytes. The actin gene family is a noteworthy exception because its evolution has been inferred in studies (Meagher *et al.*, 1999; Bhattacharya *et al.*, 2000) that included a wide sampling of algae, liverworts, lycophytes, moniliforms and seed plants.

The phylogenetic framework we discuss here underscores the importance of appropriate taxon selection when inferring the evolution of developmental genes, including the detection of gene duplication and functional shifts (Eizinger *et al.*, 1999; Ganfornina and Sanchez, 1999; Holland, 1999; Wray, 1999; Kellogg, 2000b). A denser and more diverse phylogenetic sampling is a critical issue in studies of the evolution of development (Browne *et al.*, 2000; Hughes and Kaufman, 2000; Wray, 2000) because it is essential to distinguish convergence, parallelism and reversal. There is an obvious positive trend to broaden taxon sampling, and several aspects need to be considered in selecting new 'model' organisms: phylogenetic position, developmental mode and experimental practicality (Hughes and Kaufman, 2000). Our phylogenetic framework, which includes statements about the relationships of taxa (phylogenetic statements) and the character state changes that support lineages (taxic statements), provides a sound basis for selecting additional taxa that are critical in studies of the evolution of plant development.

17.6.3 Significance of phylogenetic studies in evolutionary developmental biology

Phylogeny estimation is best approached by analysing DNA sequence data and/or morphological data (de Queiroz, 2000; Hillis and Wiens, 2000; Thornton and DeSalle, 2000). The evolution of development should be evaluated by comparing these independent data sources and their resultant trees with phylogenies generated from developmental genes. A step-by-step procedure that advances from an estimate of phylogenetic relationships, to the reconstruction of morphological character evolution, and finally to the identification of evolutionary changes in development is recommended for moving towards a synthesis of developmental and evolutionary biology.

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