Annual Plant Reviews Volume 45: The Evolution of Plant Form

Chapter · January 2013

DOI: 10.1002/9781118305881.ch4

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Annual Plant Reviews (2013) **45**, 115–140 http://onlinelibrary.wiley.com
doi: 10.1002/9781118305881.ch4

Chapter 4

EVOLUTIONARY MORPHOLOGY OF FERNS (MONILOPHYTES)

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Abstract: Throughout its long history, concepts of plant morphology have been mainly developed by studying seed plants, in particular angiosperms. This chapter provides an overview to the morphology of ferns by exploring the evolutionary background of the early diversification of ferns, by discussing the main structures and organs of ferns, and finally by exploring our current knowledge of fern genomics and evolutionary developmental biology. Horsetails (Equisetopsida) and whisk ferns (Psilotales) are treated as part of the fern lineage. Throughout the chapter, I employ a process-oriented approach, which combines the process orientation of the Arberian Fuzzy Morphology with the process orientation of Darwinian evolution as reflected in current phylogenetics.

Keywords: Arberian Fuzzy Morphology; meristems; phylogenetics; evolutionary simplification; synapomorphy; root; telome theory.

4.1 Introduction

Ferns are one out of three extant lineages of vascular plants and form the sister clade to the seed plant lineage (Figure 4.1; Pryer *et al.* 2001). They comprise five extant lineages, namely, the leptosporangiate ferns, the marattioid ferns, the horsetails, the ophioglossoid ferns, and whisk ferns (Pryer *et al.* 2001; Smith *et al.* 2006). These five lineages show a remarkable range of morphological differentiation in the body plans of the sporophytes and to a lesser extent the gametophytes (Schneider *et al.* 2002, 2009; Pryer *et al.* 2004). It is, therefore, not surprising that the monophyly of this lineage was only recently widely accepted as a result of research efforts following the principle of reciprocal illumination by integrating fossil evidence (Stein *et al.* 1984; Stein 1993; Kenrick & Crane 1997), DNA sequence variation (Pryer *et al.* 2001, 2004;

Annual Plant Reviews Volume 45: The Evolution of Plant Form, First Edition.
Edited by Barbara A. Ambrose and Michael Purugganan.

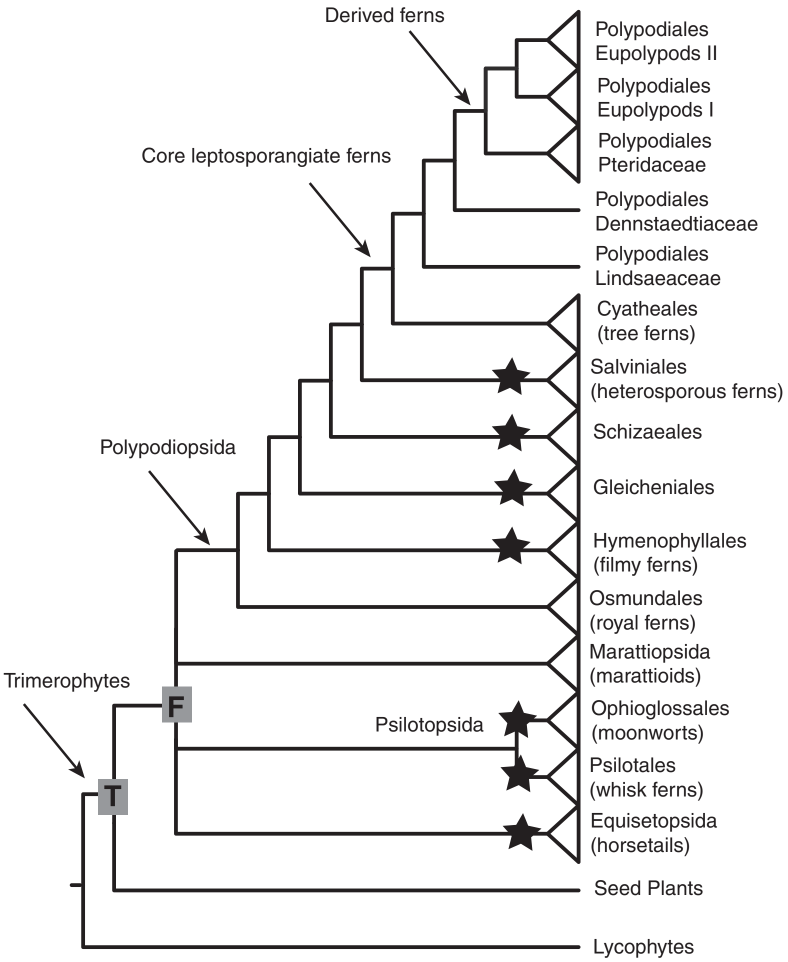

Figure 4.1 Phylogeny of ferns illustrating the current uncertainty about the early diversification of this lineage. Gray box T: indicating putative synapomorphies, for example, euphyll and RAM/SAM differentiation, shared by the offspring of the Trimerophyte lineage; gray box F: indicating putative synapomorphies, for example, apical growth of the euphyll, of the fern lineage. Stars indicate occurrences of deviations from a regular body plan differentiated into leaves, roots, and shoots. The body plan of horsetails is characterized by highly reduced euphylls that are arranged in whorls consisting of more than three leaves; the leaves of Gleicheniaceae and to some extent other families of Gleicheniales are characterized by an unusual pseudodichotomous branching and a habit resembling the shoot of some seed plants; filmy ferns (Hymenophyllaceae, Hymenophyllales) are not only characterized by the reduction of the leaf cuticula and lamina, but some clades show also a reduction of the roots or a loss of roots (e.g., *Crepidomanes*, *Didymoglossum*, *Gonocormus*) as well as a clear differentiation of leaves and shoots (*Gonocormus*); the winding leaf of the schizaealean fern *Lygodium* shows shoot-like features; moonworts (Ophioglossales) have a reduced root system and an unusual position of the sporangia; and whisk ferns (Psilotales) are characterized by the lack of roots, the reduction of leaves, unusual position of sporangia, and shoot-like organs best described as misfits.

Wikstroem & Pryer 2005; Qiu *et al.* 2006, 2007; Schuettpelz Korall & Pryer 2006; Karol *et al.* 2010; Rai & Graham 2010), and the morphological variation of extant taxa (Schneider *et al.* 2009). The lineage is sometimes called monilophytes based on the term Moniliformopsis introduced by Kenrick and Crane (1997) but I use here the term ferns instead following Pryer *et al.* (2004). Despite the differences of the body plans, ferns share several important features including a life cycle in which both generations, the usually haploid gametophyte and the diploid sporophyte, are free living and differ substantially in their body plans from each other (Schneider *et al.* 2002, 2009). The only exception is formed by the heterosporous waterferns, which are a rather species-poor lineage nested within the lineage of leptosporangiate ferns (Pryer *et al.* 2004). The gametophyte of ferns tends to be dimidiate and of a simple body plan, whereas the sporophyte develops a complex body plan that includes the differentiation into shoot, root, and leaves. In morphological complexity, the sporophyte of ferns is comparable to the sporophyte of seed plants, however, considerable differences exist such as the absence of secondary growth in extant ferns, the lack of a bipolar orientated embryo, and variation in shoot branching (Schneider *et al.* 2002, 2009).

In this review, I try to provide an overview on the current knowledge and to identify the major questions to be studied using phylogenetics and/or developmental genetics in the near future. I have approached this via two different perspectives: (1) a lineage and time-oriented perspective and (2) a morphological structure-based perspective. Finally, I review our limited knowledge on the developmental pathways in ferns and the need to sequence a whole fern genome.

Throughout the chapter, I refer to the vast body of literature on plant morphology. To avoid repetition, I want to point out some of the most comprehensive references concerning the morphology of ferns: Bierhorst (1971), Bower (1923, 1935), Campbell (1911), Goebel (1928/1930), Guttenberg (1965), Ogura (1972), Schoute (1938), Troll (1937), and Velenovsky (1905).

4.2 Context of evolutionary plant morphology

It is important to evaluate the context when interpreting fern morphology. Classical plant morphology has always experienced problems with ferns because the typological concept of roots and leaves had been developed on the model of the "Urpflanze," which is an essentialist representation of a eudicot angiosperm (Kaplan 2001a, 2001b). Ferns may be qualified as misfits in the context of typological/essentialistic morphology. I do not refer here only to extremes such as the sporocarp of waterferns (Nagalingum *et al.* 2006), the winding leaf of *Lygodium* (Mueller 1982), nonappendicular leaves found in some filmy ferns (Bierhorst 1973), and the "stolons" of *Nephrolepis* (Richards *et al.* 1983) but the fern body plan(s) in general. Some authors raised correctly the question if ferns are really cormophytes (Hagemann 1976, 1992, 1997).

I want to illustrate this with three examples. Firstly, the leaf of the majority of ferns share characteristics with shoots as a result of a dominant acropetal growth instead of a basipetal growth found in most angiosperm leaves (Reiser *et al.* 2000; Schneider *et al.* 2002, 2009). Secondly, ferns show a range of branching patterns in comparison to the highly conserved origin of secondary shoots in the leaf axils of seed plants (Bierhorst 1973; Hagemann 1976, 1989). Thirdly, the embryo is not organized in a bipolar fashion and, therefore, Goebel (1928/1930) introduced the term of primary "homorhiz" for ferns because its primary root is short-lived or perhaps not definable (Gutenberg 1965).

A more appropriate approach to interpret fern morphology is without a doubt offered by the concept of "continuum morphology" or "Aberian Fuzzy Morphology" (Sattler 1996; Rutishauser & Isler 2001; Kirchoff *et al.* 2008). It is remarkable that representatives of this school have not discussed ferns in greater detail yet. As an example, continuum morphology is well suited to provide an accurate description of the leaf of ferns because this concept allows a deviation from a single "Urform." Goethe's Urpflanze has three well-differentiated organs, the leaf, root, and shoot. These three organs are seen as the three distinct and invariant modules that build up higher plants (Figure 4.2). Recently, similarities have been stressed between classical morphology and classical invariant theory (Mavroodiev 2009). Continuum morphology employs a holistic view of the plant body in which the different organs, such as leaves, shoots, and roots, are linked by shared developmental processes. In comparison to angiosperms, the leaves of ferns share important similarities with shoots and thus the differentiation between the organs may

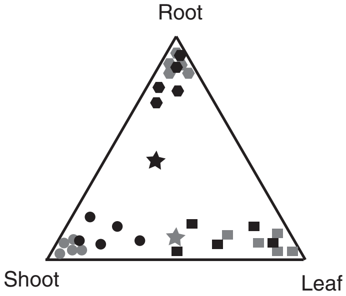

Figure 4.2 Continuum morphology concept of leaf (squares), root (diamonds), and shoot (circles) in seed plants (gray) and putative description of the differentiation of these organs in ferns (black). In general, the differentiation of shoot and leaf is lower in ferns than in seed plants despite some variation that exists especially in the context of leaves. However, leaves of ferns, for example, indeterminate growth frequently share features attributed to shoots in seed plants. Some fern leaves, for example, the climbing leaf of *Lygodium* may be best scored as a transitional form between leaf and shoot. The stars indicate the position of organs with ambiguous homology such as the stolon of the derived fern *Nephrolepis* (black star; Sanders *et al.* 2011) and the phylloclade of the monocot *Ruscus* (gray star; Hirayama *et al.* 2007).

be understood as less distinct (Figure 4.2). As an example, the leaves of many ferns show a relatively indeterminate growth that may be caused by a similar expression of transcription factors in the shoot apex and the apical meristems of the leaves/pinnae (Reiser *et al.* 2000; Harrison *et al.* 2005; Sanders *et al.* 2011). In addition, several unusual fern structures, for example, stolons of *Nephrolepis* (Richards *et al.* 1983; see also Sanders *et al.* 2011), can be best described as misfits that combine features of different organs.

It is important to keep the influence of classical morphology in mind because it is still very influential especially as a result of the remarkable efforts of Don Kaplan (2001a, 2001b) who provided access to this knowledge to a mainly English reading audience. However, classical morphology is not well aligned to the concept of Darwinian evolution. It is very important to keep in mind that the meaning of "primitive" in a typological context is not synonymous with "ancestral" in an evolutionary context. In the following, I address the evolution of ferns mainly from a perspective based on the insights of scholars, such as Willi Hennig (1965) and Walter Zimmermann (Donoghue & Kadereit 1992; Classen-Bockhoff 2001), focusing on the transformation of structures in time. This strictly phylogenetic approach is more likely to be compatible with the developmental, process-oriented perspective of the Arberian thinking than with the typological classification of classical plant morphology (Classen-Bockhoff 2001; Rutishauser & Isler 2001).

The importance of "transformation of forms" versus "fixed typology" can be illustrated with the discussion on the evolution of leaves. The origin of leaves is frequently discussed and the nonhomology of leaves of liverworts, mosses, lycophytes, ferns, and seed plants is widely accepted. However, these statements do not provide us with any understanding of the origin of leaves. Many proposed hypotheses require Goldschmidt's hopeful monsters as an explanation of the saltations proposed in the evolution of leaf-like structures as well as other structures in plants (Bateman & DiMichele 2002; Hintz *et al.* 2006; Theissen 2009). Several current scholars of plant evolution tend to underestimate the major progress achieved by Zimmermann's telome theory (Zimmermann 1959, 1965). The hypothesis proposes a sequence of transformations, for example, overtopping, plantation, and webbing/fusion, by which a dichotomously branching shoot system evolved into a megaphyll. This theory has serious limitations and some of the processes may look a bit simple in our improved understanding of the regulation of developmental processes as pointed out by many current authors (Floyd & Bowman 2006, 2007a, 2007b; Beerling & Fleming 2007; Tomescu 2008; Boyce 2010; Galtier 2010) but the "gradualistic" perspective breaks the evolution of complex organs into steps and thus it provides a concept that is actually testable, which cannot be achieved with the majority of typological-based hypotheses on the origin of leaves. Some of these processes may have involved fusion and/or substantial modifications of pathways and thus may have involved the establishment of hopeful monsters (Theissen 2009) especially if they transformed early ontogenetic stages (Rieppel 2001). I want to argue here for an approach that considers partial homology because leaves may not have originated by a single mutation creating the ultimate leaf but by a sequence of transformations. Of course, these hypothetical transformations need to be outlined under consideration of our current understanding of the regulation of plant developmental processes (Harrison *et al.* 2005; Floyd & Bowman 2006, 2007a, 2007b). Some of these transformations may have occurred before and others after the divergence of extant lineages of land plants but convergent evolution via co-opting the same ancestral gene pathways need to be considered (Harrison *et al.* 2005). A process- oriented approach, combining phylogenetic and developmental perspectives, instead of a typological-oriented approach is the most promising approach to identify the developmental pathways and their transformation in the evolution of land plants.

The phylogenetic relationships of the inferred model taxon have to be considered carefully to avoid positive misleading support or rejection of a hypothesis. Some interesting model systems, such as the highly modified body plans of some species of *Nephrolepis* (Sanders *et al.* 2011) and species belonging to the filmy fern genus *Gonocormus* (Schneider 2000) are derived members of particular fern lineages (Pryer *et al.* 2004; Smith *et al.* 2006). Thus, we need to consider the result as “secondary” modification similar to the situation of the evolution of misfits in angiosperms such as the phylloclade of the monocot *Ruscus* (Hirayama *et al.* 2007). Choosing the right model is always essential and thus the leaf development of more conservative taxa such as *Osmunda* may be more informative than highly derived systems. I point out *Osmunda* on purpose. The royal ferns, Osmundaceae, are not only the offspring of the Paleozoic radiation of leptosporangiate ferns but we also have evidence for a high conservation of the body plan of these ferns at least since the Triassic (Taylor *et al.* 2009).

4.2.1 Perspective 1: rapid radiation versus stasis in the evolution of fern body plans

The evolution of fern body plans is best summarized by employing the concept of two major phases as it was established in studies on the evolution of other major branches of life, for example, the evolution of angiosperm flowers (Endress 2001). The first phase is best visualized with the scenario of an explosive radiation of very divergent body plans whereas the second phase is characterized by conservation of a few of these body plans. The later process may be described as canalization. Ferns are especially suited to study these phases because in contrast to seed plants, the modern lineages still contain remnants of this explosive phase of morphological radiation whereas in seed plants older forms were consistently replaced by more derived forms (Figures 4.1 and 4.3).

The explosive phase started with the replacement of the trimerophyte by two daughter lineages, the seed plants and the ferns (Kenrick & Crane 1997;

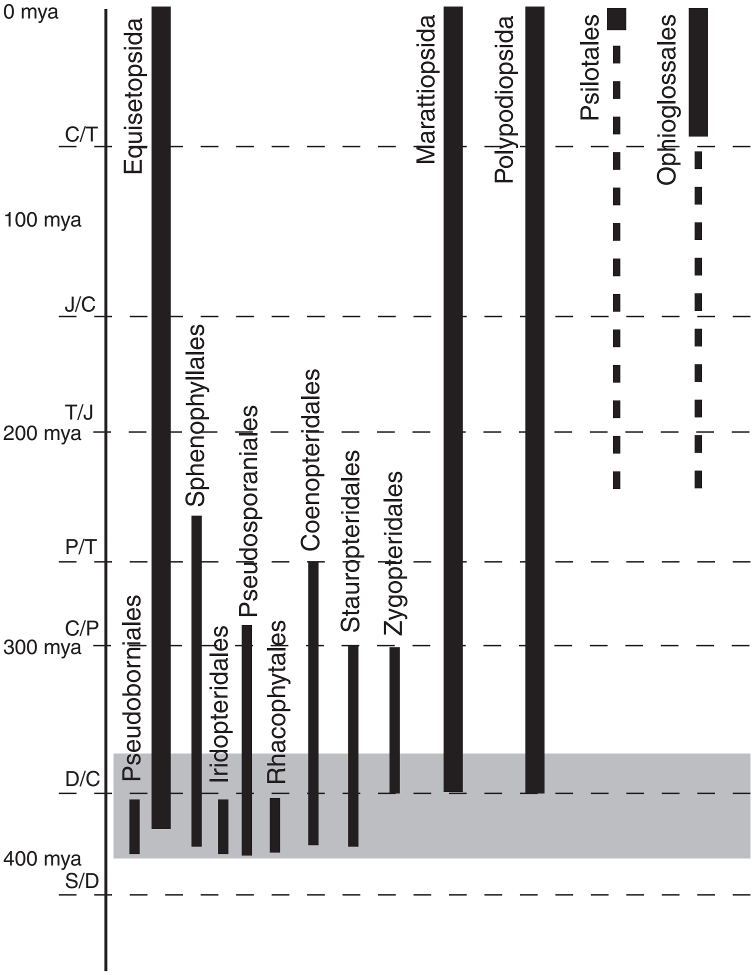

Figure 4.3 Overview about the time occurrence of lineages recognized within the monilophytes (following Taylor *et al.* 2009 with the exception of Ophioglossales and Psilotales). Gray box indicates the time of the early radiation of ferns. Dashed vertical lines indicate the borders between major geological periods: S/D, Silurian–Devonian Transition; D/C, Devonian–Carboniferous Transition; P/T, Permian–Triassic Transition; T/J, Triassic–Jurassic Transition; J/C, Jurassic–Cretaceous Transition; C/T, Cretaceous–Tertiary Transition (KT boundary).

Taylor *et al.* 2009). Both sister lineages underwent a rapid diversification in the Devonian in which a vast number of morphologically diverse lineages evolved (Figure 4.3). In the early Carboniferous, the body plans of the three lineages with a sufficient fossil record, namely, the leptosporangiate ferns, the marattioids, and the horsetails, had been established whereas many Devonian groups went extinct. The origin of the two other body plan groups, the ophioglossoids and the whisk ferns, is unclear because these sister lineages form a ghost lineage lacking a fossil record in the Mesozoic and Paleozoic (Schneider *et al.* 2002; Taylor *et al.* 2009). The identification of their Paleozoic ancestors would be one major breakthrough in our understanding of fern evolution.

The body plans of the five extant lineages share several major features such as the dominance of the sporophyte, the absence of secondary growth, relatively simple meristems, and shoot systems differentiated into a long-lived, mostly branched shoot axis and leaves (Schneider *et al.* 2002, 2009). However, they differ strongly in other aspects such as the morphology of the leaves (Section 4.4, see "Mature Sporophytes"), the location of the sporangia on the leaves, for example, dorsal or marginal position at the lamina, and the kind of indumenta. Ferns show a remarkable variation in the density and composition of the indumenta. Hairs and/or scales usually densely cover young fern leaves and the shoot apices as a protection. Hairs are unicellular to multicellular structures developed from a single epidermal basal cell, whereas scales are multicellular planar structures formed by a group of epidermal cells arranged in a line. Nearly all fern indumenta can be classified either as hairs or scales with the exception of some bristle like structures developed from more than one epidermal cell but without a dorsiventral organization as in scales found in a few fern groups. Most of the ferns also possess well-developed root systems (Schneider 1996) though they are absent in the whisk ferns, but this is arguably a secondary loss in the evolution of this lineage (see Section 4.2.2.4, page 128). The explosive phase shows an overwhelming morphological diversity when the fossil record of the group in the Devonian is taken into account. These groups show a remarkable range of variation in axis organization and more or less leaf-like appendages. A particularly well-known group, the zygopterids (Zygopteridales) had elaborate, three-dimensional fronds with pinnae arranged in four ranks. Thus, the rachis had a radially symmetric cross-section instead of the usual dorsiventral organized rachis of extant ferns (Taylor *et al.* 2009). The relationships of many of these groups are still poorly understood. In some cases, testable hypothetical relationships have been proposed based on the similarities of the shoot organization such as the putative sister relationship of the Sphenophyllales to the horsetails (Taylor *et al.* 2009) or Stein's hypothesis concerning the putative origin of horsetails of ferns from a common ancestor (Stein *et al.* 1984). I want to refer here to the exquisite review of our knowledge given in Taylor *et al.* (2009) for further reading. However, I also want to explicitly express the need for a cladistic study of ferns following the approach adopted by Kenrick and Crane (1997) to study the relationships of land plants. This kind of analysis will provide a hypothesis of character states transformation based on a rigorous distinction of apomorphic, homoplastic, and plesiomorphic character states as applied successfully since the introduction of cladistic methodology in evolutionary/ taxonomic sciences.

4.2.2 Perspective 2: key structures and organs of fern body plans

In this part, I address our knowledge on four key structures of fern morphology. The focus is on vegetative components and only limited consideration is given to reproductive structures and their evolution.

4.2.2.1 Meristems

Ferns show rather simple organized apical meristems (White & Turner 1995; Imaichi 2008). Usually, they contain a single apical cell. In a few taxa, such as Marattiaceae and Osmundaceae, the larger size of the apical meristem results in the formation of an apical cell group instead of a single one. At the sporophyte level, three kinds of apical meristems can be differentiated. The shoot apical meristem (SAM) has usually a prominent apical cell of a tetrahedral shape in most ferns. The SAM functions as the initial for the entire shoot. The organization of the SAM with a singe apical cell is correlated with the lineage specific plasmodesmatal networks, which contrasts ferns to seed plants with their multicellular SAMs with interface specific plasmodesmatal networks (Imaichi 2008). The leaves of ferns usually have meristems formed around a leaf apical cell with two cutting faces or very rarely three cutting faces. The leaf apical meristem (LAM) resembles fern SAMs in having high plasmodesmatal densities. The activity of the LAM results in the formation of a marginal blastozone, comparable to those found in seed plants (Hagemann & Gleissberg 1996; Hagemann 1997). However, this marginal meristem tends to be frequently fractionated resulting in the formation of pinnae and pinnules instead of simple blades. Future studies will need to discover the role of the regulation of the apical growth in this process. In ferns, entire leaf laminas are not uncommon but the majority of ferns tend to have leaves with highly divided laminas. The roots of ferns grow with an apical meristem (RAM, root apical meristem) formed by a single tetrahedral apical cell with four cutting faces (e.g., Guttenberg 1965; Ogura 1972; Gifford 1991; Schneider 1996). One face produces the initials for the calyptra (root cap) whereas the other faces form the initials for the root body. The division process is highly conserved and results in the formation of traceable cell lineages, which makes root development different from leaf and shoot development. Traceability of cell lineages in roots of euphyllophytes has been frequently taken as an advantage to study the control of root development in various organisms including *Arabidopsis* (e.g., Menant *et al.* 2007; Saint Savage *et al.* 2008; Sozzani *et al.* 2010). The gametophyte has again an apical meristem (gametophyte apical meristem (GAM)) with an apical cell with usually two cutting faces. The formation of a marginal blastozone is visible in some larger dorsiventrally organized gametophytes (Raghavan 1989; Hagemann 1997; Imaichi 2008).

4.2.2.2 The gametophytes

The morphological variation of fern gametophytes, called prothallia, is frequently ignored in developmental studies although a lot of documentation of this variation has been achieved (Nayar & Kaur 1971). The prothallia are usually small and ephemeral. They are simple plant bodies of either radially symmetric organization such as the gametophytes of ophioglossoid ferns and whisk ferns, filamentous such as the gametophytes of horsetails and some leptosporangiate ferns, or dorsiventrally organized such as the gametophytes of marattioids and most leptosporangiate ferns (Nayar & Kaur 1971). Most dorsiventral organized gametophytes show a symmetric heart shape but they can also be asymmetric or forming thalloid strap-shaped or filamentous structures (Nayar & Kaur 1971; Takahashi *et al.* 2009). Although, radially symmetric gametophytes are always multilayered, dorsiventrally organized gametophytes usually show only a single cell layer. However, a several cell layer thick central ridge can be found in the heart-shaped gametophytes of some basal leptosporangiate ferns (Osmundaceae) and the marattioids (Nayar & Kaur 1971). More recently, some researchers studied the role of the apical meristem and marginal growth in the alteration from cordate, symmetrical to strap-like asymmetrical gametophytes in the evolution of derived ferns such as *Leptochilus* (*Colysis*) *decurrens* (Takahashi *et al.* 2009).

The development of fern gametophytes has been studied for a long time, but we still do not understand the control of the phenotype development by the genotype, which comprises the information for both the gametophyte and sporophyte. This question has been targeted by many experimental studies and it is impossible to provide a full summary here (Raghavan 1989; Sheffield 2008). Some studies speculated about the impact of haploid versus diploid genomes but this has not been confirmed by observations in ferns that display apogamy (Raghavan 1989; Bell 1992; Park & Kato 2003). In these ferns, there is a lack of sexual reproduction and the gametophyte and sporophyte have the same chromosome number.

Besides the parenchymatic cells of the core body, fern gametophytes comprise a few other cell types. Firstly, they have rhizoids that are structurally similar to root hairs. Rhizoids are likely a plesiomorphic feature in vascular plants and root hairs may have evolved by a heterotopic mutation (Schneider *et al.* 2002). Rhizoid-like hairs are also found on the scales of some derived ferns (Bower 1923) and their origin may be a further case for heterotopic mutations in ferns. The origin of these structures has not been studied so far and hence this hypothesis was not fully developed previously to my knowledge. Fern gametophytes also may bear hairs, in particular glandular hairs (Nayar & Kaur 1971). The genes controlling the formation of these hairs may be the same controlling hair formation on the sporophyte shoot or leaf.

Other structures, such as archegonia and antheridia, are unique to gametophytes (Nayar & Karu 1971; Raghavan 1989). Gemmae and other forms of vegetative buds can be found in both generations (e.g., Bower 1923; Nayar & Kaur 1971; Raghavan 1989) but an exhaustive comparative study is still missing.

In summary, the gametophyte shares some cell types with the sporophyte, for example, undifferentiated parenchymatous cells forming the main body of the gametophyte, rhizoids, and hairs but the gametophyte usually lacks other cell types such as tracheids and phloem cells.

4.2.2.3 Embryos

Ferns show a remarkable variation of the structure of the embryo (Figure 4.4; Johnson & Renzaglia 2008, 2009). However, the embryo does not show a bipolar organization as found in seed plants (Guttenberg 1965; Bierhorst 1971; Schneider *et al.* 2002). Instead, fern embryos show a division into a usually large foot area and an embryo body that includes the formation of a somewhat bended vascular axis connecting the embryonic SAM and LAM with the RAM. The shoot meristem extends to the permanent shoot system whereas the embryonic root is short lived and gets replaced by other roots formed by tissue originating from the SAM. This situation was described as primary "homorhiz" (Goebel 1928/1930) because root systems of ferns lack a permanent primary root. In addition, the leaves gradually develop to more complex leaves starting from rather simple, often undivided leaves with a short petiole and a forked vein to more complex leaves, via step-by-step increase of the complexity in the sequence of leaf formation.

The variation among the embryos of vascular plants is remarkable although some structures appear highly conserved. All homosporous vascular plants appear to possess a foot, which plays a critical role to connect the young embryo and the gametophyte (Duckett & Ligrone 2003; Johnson & Renzaglia 2008, 2009). The foot is absent in seed plants, which is likely correlated with the evolution of seeds. Likewise, the conservation and variation of the suspensor is probably correlated with the evolution of seeds. It would be really interesting to compare the role of genes known to regulate embryo patterning in *Arabidopsis* to those in ferns (Izhaki & Bowman 2007). It is interesting to recognize the distinction of the embryos of horsetails (Equisetopsida) and whisk ferns (Psilotales) in comparison to their relatives (Figure 4.4). This may suggest an early ontogenetic deviation causing the highly distinct body plans of these lineages. The modification of embryo development may provide an explanation for the origin of body plans that appear less compatible with scenarios of gradualistic stepwise transformation. Thus, they may be "hopeful monsters" comparable to turtles (Rieppel 2001).

4.2.2.4 Mature sporophytes

The body plans of most ferns are composed of three organs: leaves, roots, and the shoot. The shoot is usually called a rhizome despite the range of variation in growth forms including long-creeping rhizomes, short-erect rhizomes, and tree-like rhizomes (Bierhorst 1954). This organ structure reminds one of seed

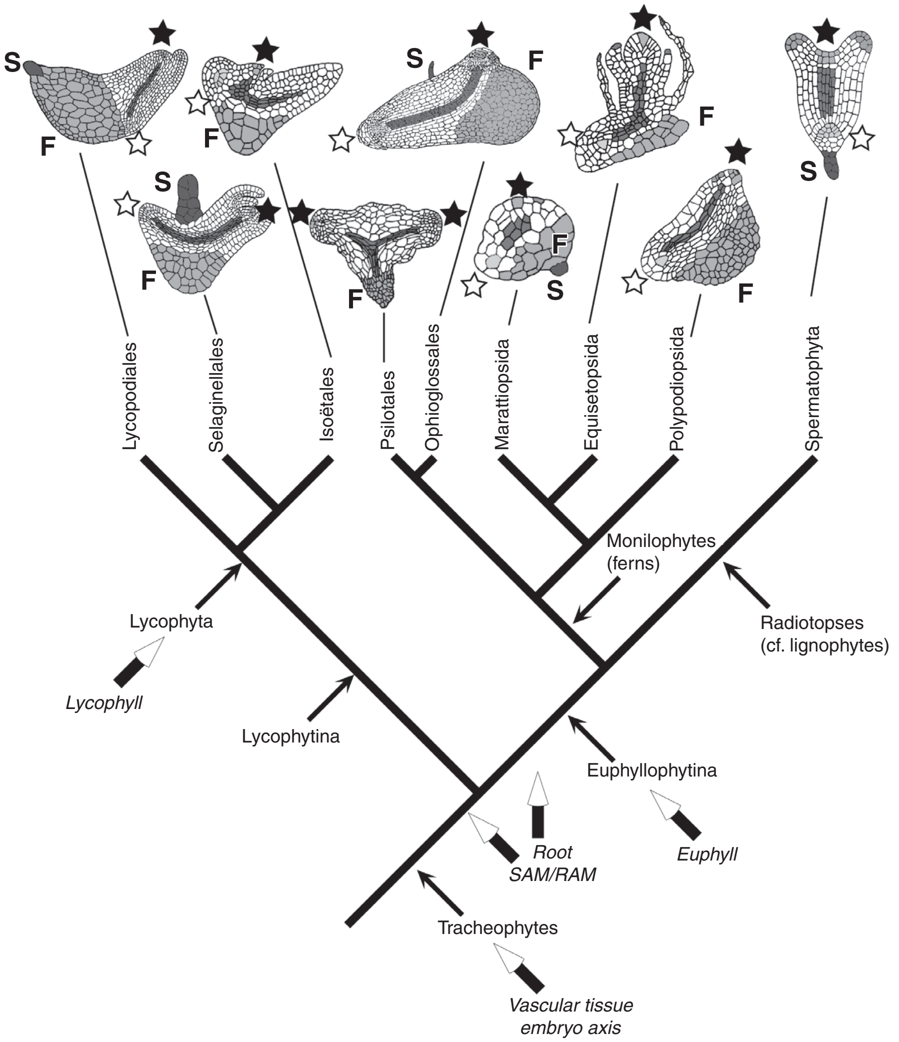

Figure 4.4 Evolution of embryos in vascular plants, plotted onto a phylogenetic hypothesis proposed by Pryer *et al.* (2001). The graphics have been redrawn from descriptions of fern embryos obtained in studies carried out in the nineteenth and twenty-first centuries (Guttenberg 1965; Bierhorst 1971). The examples were chosen to represent the variation among lineages of vascular plants. In lineages with considerable variation such as Ophioglossales, the chosen example represents the majority of embryos described so far. As an example, in the Ophioglossales embryos of closely related species may differ in the absence/presence of a suspensor, size of the foot, and the geometry of the embryo. In other lineages, for example, Polypodiopsida, the variation among described embryos is limited and embryo shown likely represents the ancestral state of the lineage. The bipolar embryo of seed plants is unique and characterized by the absence of a foot, which likely coincides with the evolution of seeds. Among seed plants, the embryo structure can be very different but the bipolar structure is one of the apomorphic characters of the seed plant lineage. *Note*: the embryos are not shown at the same stage of their development and are not shown proportionately.

plant shoots but it is still unclear if this differentiation happened before or after the separation of the monilophyte and seed plant lineages. It is important to recognize that leaves of ferns share the apical growth with the shoot and thus these two organs are less differentiated from each other than those found in extant seed plants. However, it is not clear yet if this difference is caused by independent origins as suggested by some authors or transformations that postdate a shared origin. Another major difference with seed plants is the variation in the processes of lateral shoot formation. In some ferns (e.g., *Gleichenia* and *Lygodium*), the rhizome branches dichotomously and thus leaf initiation is independent from lateral shoot initiation (Bierhorst 1973; Hagemann 1989). However, in the majority of ferns, the initiation of a lateral shoot is dependent on the formation of lateral leaves although they are usually not formed in the leaf axil. Most interesting are those ferns that seem to be able to form leaf–shoot complexes, such as in some Dennstaedtiaceae and filmy ferns, that are challenging the notion of two different developmental programs (Bierhorst 1973; Hagemann 1989). I need to stress again that these may be secondary modifications (character state is not ancestral for ferns), which could provide us with interesting insights into the evolution of developmental pathways. The formation of lateral branches is thus more variable than in seed plants, which may be best described as less constrained. The level of variation can be best illustrated by pointing out two unusual patterns in *Angiopteris* and ophioglossoids. Relatively little attention has, so far, been given to the formation of new shoots in the marattioid genus *Angiopteris*. Here, buds originate from serial dormant meristems along the stipules at the base of the leaves (Campbell 1911; Huang *et al.* 2011). This unique structure resembles similar arrangements in some angiosperms but it has very likely evolved independently. Similarly, the unusual body plan of ophioglossoids has not found as much attention as they require (Campbell 1911). The compact shoot produces usually only a single leaf per growing period despite the initials for the next leaves already being fully formed (Bierhorst 1977; Schneider *et al.* 2002). Ophioglossoid shoots rarely or never form lateral shoots but the leaves bear very unusual fertile structures. These also arise in the axil of the leaf and have been variously interpreted. Finally, it is important to

Figure 4.4 (*Continued*) It is important to note the high level of variation supporting the notion of limited conservation of embryology in the early diversification of ferns. It is interesting to note the distinctive embryos of the Equisetopsida and Psilotales, suggesting substantial changes in their early ontogeny that likely contributes to their distinct body plans. Putative shared synapomorphies are plotted on some deeper nodes. Roots originated either before the split of lycophytes and trimerophytes or evolved at least twice. Lycophylls and euphylls are two independent events in the evolution of vascular plants. SAM, black star—shoot apical meristem; RAM, open star—root apical meristem; F, foot; S, suspensor; dark central area of embryos—vascular tissue—embryo axis. Simple arrows indicate lineages, open arrows indicate putative origins of structures.

note that all extant monilophytes lack secondary growth despite the fact that some Paleozoic monilophytes may have had secondary growth (Taylor *et al.* 2009). In general, secondary growth was always rare in this lineage including monilophytes with tree-like habits, for example, tree ferns and the Paleozoic genus *Psaronius* (Taylor *et al.* 2009). Similar to palms, ferns evolved structural innovations that allowed them to form erect trunks of heights more than 20 m (Large & Braggins 2004). These innovations include the formation of root mantles, highly dissected steles, and organization of mechanical tissues (Ogura 1972; Large & Braggins 2004).

Nearly all monilophytes possess a root system. All roots can be classified as shoot born with the exception of the root of the embryo (Figure 4.4). However, the later is short lived and thus the root system of ferns is best described as rather uniform, for example, "homorhiz" (Goebel 1928/1930). Most fern roots branch via the lateral roots, which form endogenously from the endodermis or pericycle (Schneider 1996). This condition resembles the lateral root formation of seed plants. Dichotomously branching roots can sometimes be found in the ophioglossoid ferns but the roots of these ferns are usually unbranched (Campbell 1911; Bierhorst 1971; Schneider *et al.* 2002). All fern roots possess a root cap (calyptra) and nearly all form root hairs (Schneider 1996; Schneider *et al.* 2002, 2009). The later are lacking in the roots of ophioglossoids. Roots are completely lacking in the Psilotales, in the aquatic heterosporous fern genus *Salvinia* and some epiphytic/saxicolous species of filmy ferns (Schneider 2000; Schneider *et al.* 2002, 2009). The lack of roots in these cases is likely the result of evolutionary simplification of the body plan and not an ancestral condition. Many shared similarities indicate a shared origin of roots in the ancestor of ferns and seed plants but these similarities may be also explained by co-option of similar genes or developmental pathways. As an example, the pathway controlling the differentiation of the rhizodermis (epidermis of the root) is similar to the pathway controlling the differentiation of the epidermis (Schiefelbein *et al.* 2009; Pu & Brady 2010). In addition, the developmental pathway controlling the development of root hairs in angiosperms appears to have been co-opted from the pathway controlling the differentiation of rhizoids in bryophyte gametophytes (Menand *et al.* 2007; Jang *et al.* 2011).

Fern leaves grow mainly via an apical growth, which is most visible in the circinate development of the unfolding leaf (Schneider *et al.* 2002, 2009). The persistence of apical growth can result in the development of rather large leaves of several meters long as illustrated by the long twining leaf of the fern genus *Lygodium* (Mueller 1982). It is the only example in the plant kingdom where the plant climbs via a winding leaf instead of winding shoots. Again, this illustrates the fuzziness of the leaf concept defined for angiosperms when applied to ferns. However, the majority of fern leaves are well defined in their length and some are rather small. Extremely small leaves, such as the scale-like leaves of horsetails (Equisetopsida) and whisk ferns (Psilotales) have been the focus of previous controversies (e.g., Bierhorst 1977; Kaplan 2001b;

Schneider *et al.* 2002, 2009). They were classified as microphylls together with the leaves of lycophytes. However, Kaplan (2001b) showed in a comprehensive typological argument that the concept of microphylls is deeply flawed. This is consistent with the phylogenetic evidence of independent origins of so-called microphylls (Kenrick & Crane 1997). Here, I suggest refusing the division of the leaves of vascular plants into micro- and megaphylls. Both terms are problematic and contribute to confusions (e.g., Kaplan 2001b). Thus, I suggest that a new terminology, such as lycophylls and euphylls, would help to circumvent misunderstandings.

Lycophylls: Leaves of extant and extinct members of the lycophyte lineage that originated from ancestors such as *Drepanophycus*. Crane and Kenrick (1997) argued that these leaves might originate from sterile sporangia. This hypothesis still needs further testing especially in respect to the origin of genes controlling the differentiation of dorsiventral organs such as leaves (see Harrison *et al.* 2005). In angiosperms, the YABBY genes play a critical role but no copy of this family has been found in seed-free land plants (Efroni *et al.* 2010; Floyd & Bowman 2010; Sarojam *et al.* 2010). In this context, it is important to note that the sporangia of lycophytes show a dorsiventral organization in contrast to the sporangia of all other land plants, which show a radially symmetric organization (Kenrick & Crane 1997; Schneider *et al.* 2002, 2009). Lycophylls usually have a single unbranched vein but some exceptions exist within the genus *Selaginella* (Wagner *et al.* 1982).

Euphylls: Leaves of monilophytes and seed plants share features such as a more or less defined growth, the formation of leaf gaps in the stele of most taxa, and dorsiventral organization. The shared ancestral stages are described with the term pseudodichotomous branching or lateral branch systems (Floyd & Bowman 2010). The concept of euphylls differs substantially from the megaphyll concept because the concept aims to determine the shared ancestral character states (synapomorphy) and assumes subsequent transformations as independent such as the differentiation of lamina and petiole. This differentiation evolved at least twice during the diversification of the trimerophytes (ancestors of ferns and seed plants; Figure 4.1). It is important to note that this concept resembles the partial-shoot theory of the leaf and similar concepts of the Arberian Fuzzy Morphology (Rutishauer & Isler 2001; Kirchoff *et al.* 2008). The concept assumes explicitly that only early steps in the process of leaf evolution have been shared among ferns and seed plants among the different lineages of ferns. The joint origin is currently outlined as a shoot system with a pseudodichotomous branching (e.g., Beerling & Fleming 2007; Kidner 2007; Floyd & Bowman 2010).

The apical growth and morphogenesis of fern leaf lamina suggests a high similarity with the morphogenesis of shoots. Some authors discussed the limitation of ferns to form a blastozone (Zurakowski & Gifford 1988; Hagemann & Gleissberg 1996; Hagemann 1997) that would allow the development and evolution of entire laminas, which may explain the high frequency of fern leaves with highly dissected laminas. Ferns may evolve entire laminas mainly by reducing the space among secondary veins or by evolving complex anatomosed venations as found in many derived fern genera such as the majority of ferns belonging to the families Polypodiaceae and Tectariaceae (Zurakowski & Gifford 1988; Hagemann 1997; Schneider *et al.* 2009). Ferns can prove to be a powerful system to investigate the correlation between changes in developmental pathways and changes in leaf morphology. Sometimes, individuals with once pinnate or bipinnate laminas can be found in the same species (e.g., several species of *Asplenium*). In addition, hybrids can be generated between simple bladed species and bipinnate species such as the hybrid between the simple-bladed *Asplenium nidus* and the bipinnatifid *Asplenium prolongatum* (N. Murakami, personal communication) and *Asplenium* × *hybridum* that is the hybrid between the simple-bladed *Asplenium sagittatum* and the pinnatifid *Asplenium ceterach* (Pinter *et al.* 2002). In these hybrids, the lower part of the lamina resembles the leaf of the parent with the divided lamina, whereas the upper part of the lamina resembles the leaf of the parent with the undivided lamina.

The formation of complex induments on the leaf and shoot is a further character of great importance to ferns (Bower 1923). In general, two main types are recognized: hairs and scales. Hairs are classified as uni- to multicellular trichomes formed by cell divisions of a single epidermal cell. Similar hair structures can be also found on some gametophytes. Scales are classified as multicellular, dorsiventral structures that originate by cell divisions of several epidermal cells. Some authors have speculated that scales may represent reduced leaves because they sometimes show the phyllotaxis of leaves (Stuetzel & Geiling 1997) but some transitional forms between scales and hairs are also known (e.g., Bower 1923). These transitional forms include a multicellular hair-like structure formed by several epidermal cells but with a radial organization. Interestingly, the same type of indumentum can be found on the shoot and leaf supporting the view of a continuum of leaves and shoots in ferns (Ogura 1972). Hair-bearing scales are another notable morphological curiosity found in some ferns (Schneider *et al.* 2002, 2009; Wang *et al.* 2010). These structures can resemble rhizoids in their shape but neither the function nor the homology of these structures is currently understood. Their similarity to rhizoids of the gametophyte and root hairs suggest a heterotopic mutation that results in the expression of genes controlling the rhizoid and/or root hair development at the surface of shoot scales.

At least one putative *de novo* organ can be found in ferns. The origin of the sporocarps of heterosporous ferns is still mysterious (see Nagalingum *et al.* 2006 for references) despite the recent progress with the understanding of the phylogeny of water ferns and the recognition of the homology of all sporangia-bearing structures of these ferns (Nagalingum *et al.* 2006). Sporocarps are shoot-like structures bearing the sporangia either enclosed in walls resembling seeds (Marsileaceae) or along dichotomously branched axes (Salviniaceae). In ferns, sporangia are usually formed by leaves that are equally adapted to photosynthesis (trophosporophylls). However, in some ferns leaves or parts of the leaves are differentiated with the two functions segregated to either sporophylls (leaves forming sporangia) or trophophylls (leaves carrying out photosynthesis). Sporocarps are likely not homologous to sporophylls because many of their characteristics such as location are shoot-like (see Nagalingum *et al.* 2006). In the framework of Arberian Fuzzy Morphology, sporocarps need to be interpreted as misfits that are neither leaves nor shoots. In some cases (e.g., *Salvinia*), they also show positive geotropic growths resembling roots (Bierhorst 1971; Nagalingum *et al.* 2006).

Another mystery is the origin of the sporangia bearing structures of whisk ferns (Psilotales) and moonworts (Ophioglossales) (Figure 4.1). Both lineages differ from leptosporangiate ferns (Polypodiopsida) and marattioids (Marattiopsida) by not sharing a dorsal or marginal position of the sporangia (Bierhorst 1971; Schneider *et al.* 2009). Instead, the sporangia are located on the apical side of leaves (Bierhorst 1971; Schneider *et al.* 2009). Whisk ferns possess two (*Tmesipteris*) or three *(Psilotum*) partly fused sporangia located at the apical side of forked leaves (Bierhorst 1971, 1977; Schneider *et al.* 2009). Moonworts have a single spike, with the exception of *Cheiroglossa*, which can be branched (e.g., *Botrychium*, *Helminthostachys*) or unbranched (*Ophioglossum*) arising along the upper side of the petiole or sometimes lamina (*Ophioderma*) (Campbell 1911; Bierhorst 1971; Hauk *et al.* 2003). Given the sister relationship of whisk ferns and moonworts, the hypothesis of a homologous structure requires attention in future research (see Figure 4.5). However, the alternative hypothesis of homology between the aerial structure of Psilotales and the leaf-spike apparatus of Ophioglossales requires consideration as well (Bierhorst 1977). Bierhorst (1977) based on this hypothesis of homology on the aerial structures of *Psilotum* as compared to the leaves of the leptosporangiate fern *Stomatopteris*. Finally, we also need to consider the hypotheses regarding the nonaerial creeping rhizomes of *Psilotum* as de-novo organs or as

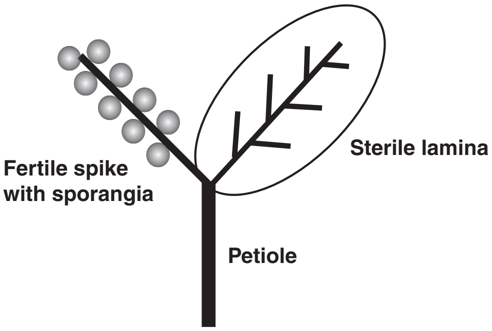

Figure 4.5 Model for the ancestral sporangiophyll of the sister lineage moonworts (Ophioglossales) and whisk ferns (Psilotales). The structure is composed of three main components: (1) a lamina, (2) a petiole, and (3) an axial structure bearing several sporangia. This morphology is found in most extant moonworts, whereas the whisk fern structure may have evolved by reduction of all three components.

homologous to rhizomes of other vascular plants (Bierhorst 1954; Takigochi *et al*. 1997).

In general, the body plan of Psilotales is very unlikely the result of the conservation of ancestral features but the result of transformations including simplifications and reductions (Schneider *et al.* 2002, 2009; Schneider 2007). The lack of roots is interpreted as a secondary reduction and not as a primary absence. This is consistent with the results of phylogenetic studies (Pryer *et al.* 2001, 2004; Schneider *et al.* 2009). In this context, it is interesting to consider the embryology of Psilotales that is likely also highly derived as indicated by very early branching (Guttenberg 1965) that is best described as pseudodichotomous (Bierhorst 1971; 1973, 1977). In this context, it is worth stressing that we still lack the description of embryos from Rhynie Chert fossils (H. Kerp, personal communication). It is evident that the lack of embryos of the otherwise completely recovered life cycle of *Aglaophyton* (Taylor *et al.* 2005) is a major draw back for the inference of ancestral embryo characters of vascular plants.

4.2.3 Perspective 3: genomics and evo-devo of ferns

With the publication of the whole genome of the spike moss *Selaginella moellendorffii*, whole genomes are now available for representatives of seed plant lineages and a lycophyte lineage (Banks *et al.* 2011). However, we are still lacking a whole genome for any fern and thus evo-devo studies on ferns rely either on candidate genes detected in the whole genome of angiosperms or the spike moss *Selaginella* or on EST or BAC libraries of selected species of ferns such as *Adiantum capillus-veneris* (Kawai-Toyooka *et al.* 2004; Yamauchi *et al.* 2005), *Ceratopteris richardii* (Rutherford *et al.* 2004), and *Pteridium aquilinum* (Der *et al.* 2011). Given the availability of whole genomes, it is not surprising that the majority of evo-devo studies are currently either focused on angiosperms such as *Arabidopsis thaliana* or the moss *Physcomitrella patens* (Rensing *et al.* 2008). In this context, it is worth noting the efforts to sequence the whole genome of the liverwort *Marchantia polymorpha*, which will have a critical impact on our ability to study the evolution of plant development and morphology (http://www.marchantia.org). The availability of whole genomes and other DNA sequencing technologies have revolutionized our understanding of plant development and its evolution such as the discovery of genes controlling the development of flowers and the discovery that the independence of the developmental pathways of gametophytes and sporophytes in *Physcomitrella* (Okano *et al.* 2009; Prigge & Bezanilla 2010). The publication of the genome of *Selaginella* will have a similar impact by providing access to the early evolution of plant development in vascular plants. However, many major questions concerning body plan evolution in euphyllophytes, the clade including angiosperms and ferns, will also require the study of ferns besides angiosperms and spike mosses (Figure 4.4). For example, comparative studies on the development of leaves in spike mosses and angiosperms will confirm the well-founded hypothesis of an independent origin of leaves in these two lineages despite the potential co-option of developmental genes in the convergent evolution of dorsiventral organized organs (Harrison *et al.* 2005, 2007; Langdale 2008). However, these insights will have a limited importance on the major challenge of leaf evolution, that is how often have leaves evolved in the euphyllophytes (Figure 4.4). This review will not focus on the evolution of plant organs in land plants because its focus is on ferns but addresses issues within ferns that can not be seen outside of the broader challenge, the evolution of plant body plans.

Several studies have assembled evidence for a shared genetic tool kit in land plants (Floyd & Bowman 2007a, 2007b) including various gene families controlling plant development such as MADS-box genes and other families of transcription factors (Hasebe *et al.* 1998; Muenster *et al.* 1997, 2008; Moyraud *et al.* 2010). Recent studies explored the genomes of the moss *Physcomitrella* and the liverwort *Selaginella* to explore the presence and copy number of genes in gene families known to be important in the regulation of plant development. In general, these studies recovered evidence for the origin of most gene families before the separation of seed plants from other land plants, with the YABBY genes as a notable exception, but also a general trend to seed plant specific gene duplications (Rensing *et al.* 2008; Banks *et al.* 2011). However, with the absence of a whole genome for any fern, we lack the ability to compare the genome of a representative of the sister lineage of seed plants that limits considerably the capability of these studies to identify seed plant specific gene duplications (Pryer *et al.* 2002).

Some studies have found evidence for independent recruitment of conserved developmental mechanisms in the evolution of plant morphology (Harrison *et al.* 2005, 2007; Langdale 2008) whereas others recovered evidence for highly conserved pathways (Schalau *et al.* 2008). Kaplan (2001a) argued for the importance of gene expression patterns in plant morphogenesis and their transformation in evolution. Ferns should be of particular interest to evolutionary developmental studies due to the mixture of highly conserved body plans as found in marattioids, highly derived transformations in other lineages such as the body plan of whisk ferns, as well as the morphological novelty, the sporocarp, found in heterosporous ferns (Nagalingum *et al.* 2006), or the climbing leaf of *Lygodium* (Mueller 1982). These studies will benefit from applying a robust phylogenetic framework as outlined in recent phylogenetic studies (e.g., Pryer *et al.* 2001, 2004; Schneider *et al.* 2009). However, the framework is still lacking the required resolution in the context of the position of horsetails, which may be sister to all other lineages of ferns or sister to one or two lineages of the fern clade (Schneider 2007; Schneider *et al*. 2009; Karol *et al.* 2010; Rai & Graham 2010). However, problems in identifying synapomorphies in the body plans of fern lineages (Schneider *et al.* 2002, 2009; Schneider 2007) may suggest a ubiquity of postlineage establishment transformation and co-option of conserved ancestral pathways in the evolution of key innovations in the evolution of fern lineages such as the innovation of sporocarps in the heterosporous water ferns (Nagalingum *et al.* 2006), rhizomes with cavities to be colonized by ants (Schneider *et al.* 2010), or the differentiation of litter collectors and trophosporophylls in the drynarioid ferns (*Drynaria*) and the genus *Platycerium* (Janssen & Schneider 2005; Schneider *et al.* 2010).

It is also worth noting that deviations from a generalized fern body plan are not restricted to horsetails and whisk ferns, but can also be found in some lineages of leptosporangiate ferns. In some cases, the existence of close relatives with regular body plans may allow the untangling of the evolution of pathways underlying these transformations such as the low level of differentiation of leaves and shoots in rootless filmy ferns of the genus *Gonocormus* (Schneider 2000). This pattern may indicate a lower level of conserved evolution of fern morphology if compared to seed plants, which will provide the opportunity to study the evolutionary processes underlying the transformation of plant morphogenesis on one hand, and will result in a challenge to differentiate between shared ancestral states, secondary simplifications, and transformation that co-opted genes of ancestral pathways to innovate new structures on the other hand. Of course, the latter question is at the center of the current discussion on the evolution of plant morphology, which resembles very much concepts of plant morphology ranging from typological concepts (Kaplan 2001a) to Aberian Fuzzy Morphology (Rutishauer & Isler 2001; Kirchoff *et al.* 2008). The integration of these concepts into comparative genomic analyses may provide us with the opportunity to address major questions of the evolution of body plans in all lineages of plants (Bowman *et al.* 2007).

Acknowledgments

Most of all, I want to thank the editors for the constant encouragement and their amazing patience with a very difficult author. I am deeply in dept to my teachers and many colleagues who discussed with me various aspects of plant morphology in particular Peter Endress (Zurich), Herbert Huber (Kaiserslautern), Don Kaplan (Berkeley), Mashiro Kato (Tsukuba), and Rolf Rutishauser (Zurich).

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