15

Fern phylogeny

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15.1 Introduction

As a consequence of employing DNA sequence data and phylogenetic approaches, unprecedented progress has been made in recent years toward a full understanding of the fern tree of life. At the broadest level, molecular phylogenetic analyses have helped to elucidate which of the so-called "fern allies" are indeed ferns, and which are only distantly related (Nickrent *et al.*, 2000; Pryer *et al.*, 2001a; Wikström and Pryer, 2005; Qiu *et al.*, 2006). Slightly more focused analyses have revealed the composition of, and relationships among, the major extant fern clades (Hasebe *et al.*, 1995; Wolf, 1997; Pryer *et al.*, 2004b; Schneider *et al.*, 2004c; Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007). A plethora of analyses, at an even finer scale, has uncovered some of the most detailed associations (numerous references cited below). Together, these studies have helped to answer many long-standing questions in fern systematics.

In this chapter, a brief synopsis of vascular plant relationships – as currently understood – is initially provided to place ferns within a broader phylogenetic framework. This is followed by an overview of fern phylogeny, with most attention devoted to the leptosporangiate clade that accounts for the bulk of extant fern diversity. Discussion of finer scale relationships is generally avoided; instead, the reader is directed to the relevant literature, where more detailed information can be found. The phylogeny presented (Figure 15.1) – which serves as a guide – integrates the results of two distinct phylogenetic analyses of fern relationships: one focused on vascular plants but emphasizing ferns (Pryer *et al.*, 2001a), the other focused specifically on overall leptosporangiate

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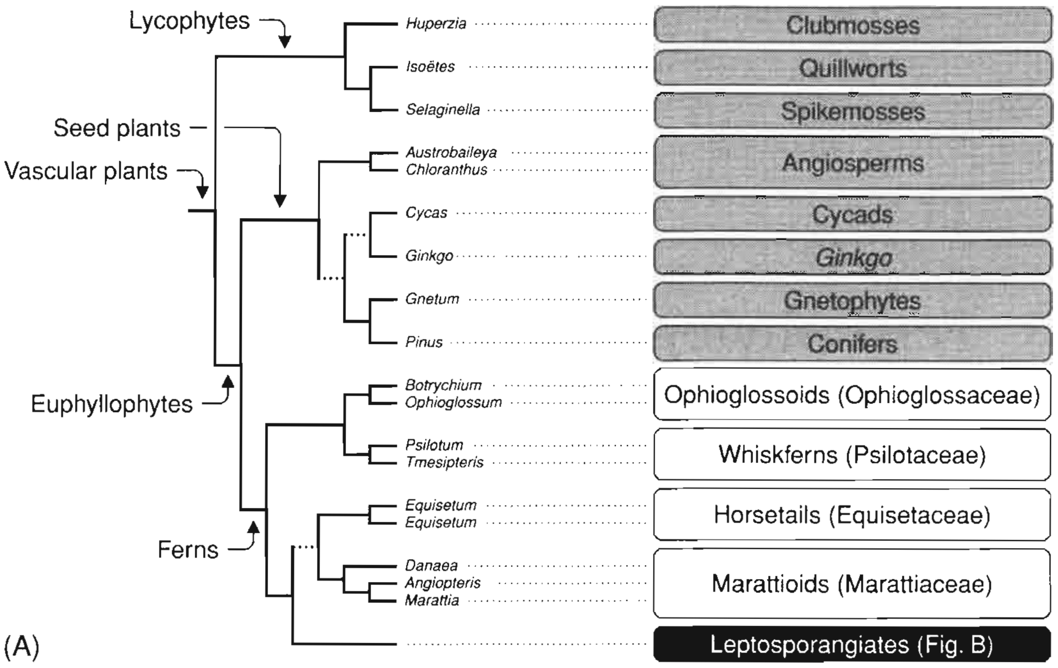
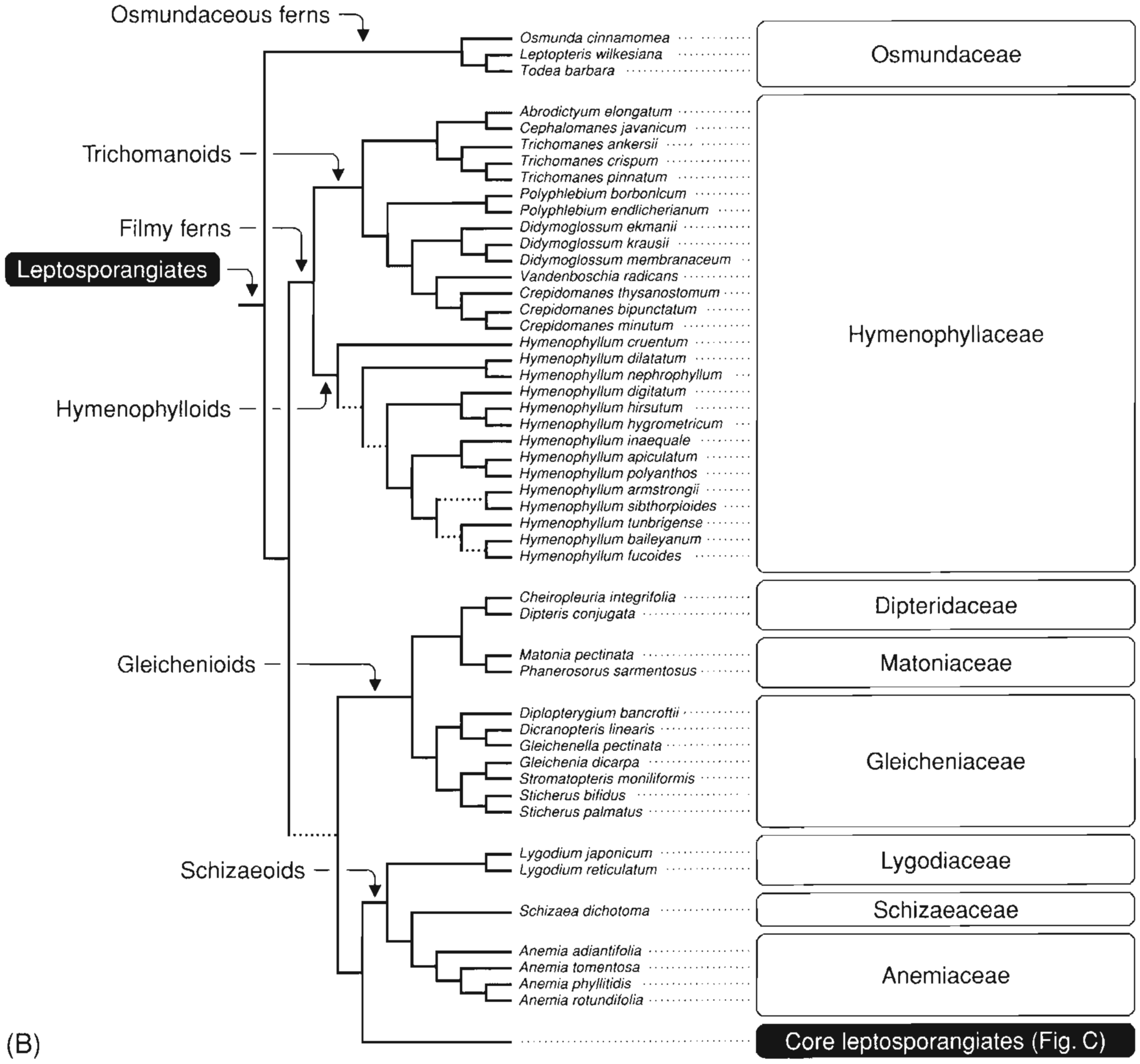


Figure 15.1 (A) Early vascular plant divergences. Phylogeny from maximum likelihood analysis of nuclear 18S and plastid *rbcL*, *atpB*, and *rps4* data (Pryer *et al.*, 2001a; leptosporangiate sampling collapsed here to a single terminal); all branches received maximum likelihood bootstrap support ≥70 except those drawn with dotted lines. Thirteen major vascular plant lineages (four of which are fern families; Smith *et al.*, 2006b) are indicated, as are other clades discussed in the text. (B–H) Leptosporangiate divergences. Phylogeny from maximum likelihood analysis of plastid *rbcL*, *atpB*, and *atpA* data (Schuettpelz and Pryer, 2007); all branches received maximum likelihood bootstrap support ≥70 except those drawn with dotted lines. Families recognized in the most recent fern classification (Smith *et al.*, 2006b; see also Smith *et al.*, Chapter 16) are indicated, as are other clades discussed in the text. (B) Early leptosporangiate divergences. (C) Early core leptosporangiate divergences. (D) Early polypod divergences. (E) Divergences within eupolypods I, part 1. (F) Divergences within eupolypods I, part 2. (G) Divergences within eupolypods II, part 1. (H) Divergences within eupolypods II, part 2.

fern relationships (Schuettpelz and Pryer, 2007). The most recent fern classification (Smith *et al.*, 2006b; Chapter 16) took the results of these studies into consideration; therefore, it is largely consistent with the phylogeny presented here.

15.2 Early vascular plant divergences

The deepest phylogenetic dichotomy among extant vascular plant lineages separates lycophytes from euphyllophytes (Figure 15.1A; Raubeson and Jansen, 1992; Kenrick and Crane, 1997; Doyle, 1998; Nickrent *et al.*, 2000; Renzaglia *et al.*, 2000; Pryer *et al.*, 2001a; 2004a; Wikström and Pryer, 2005;



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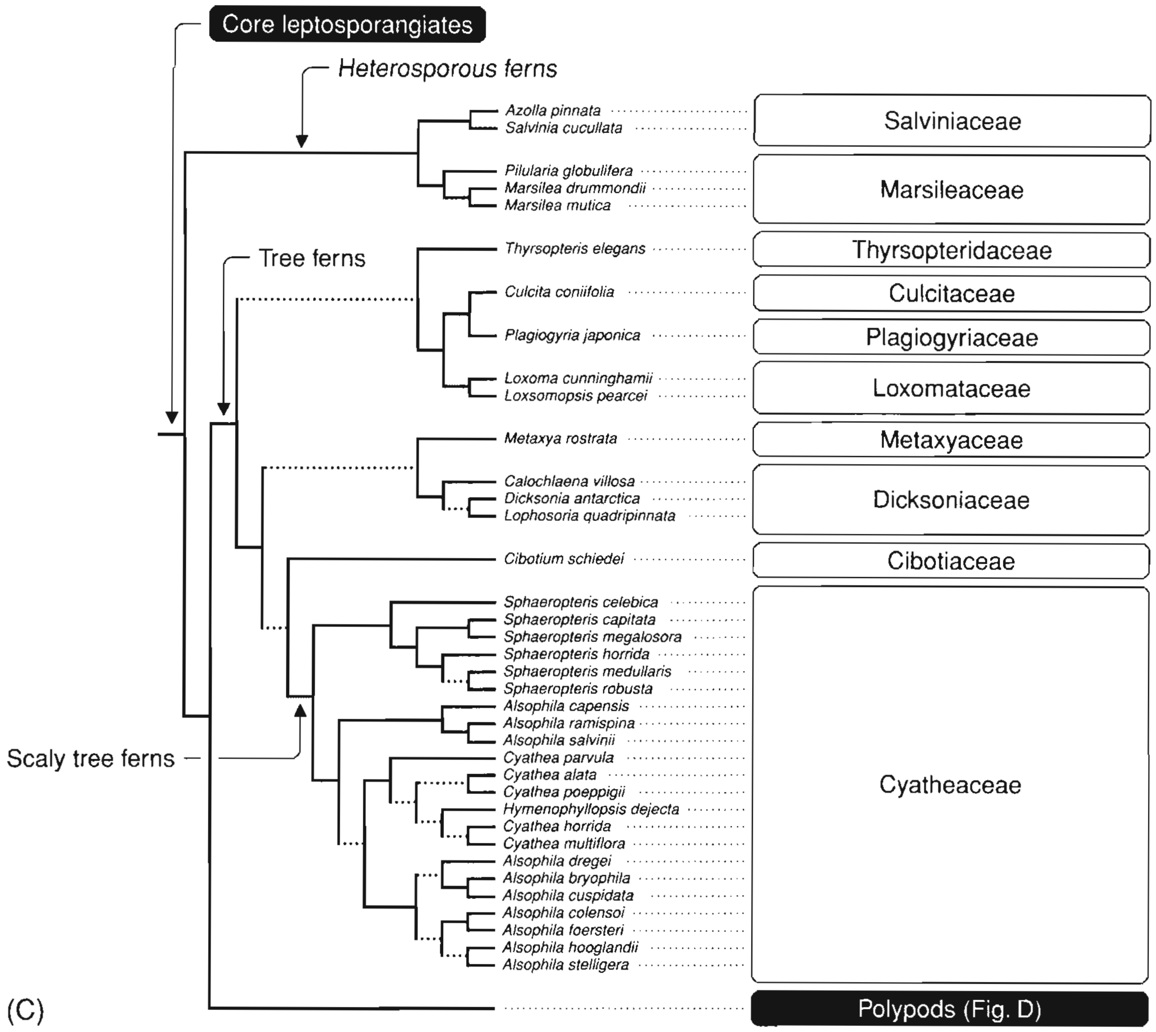
Qiu *et al.*, 2006). The lycophytes, which are characterized by lycophylls (leaves with an intercalary meristem) and account for less than 1% of vascular plant diversity, comprise three distinct lineages – the homosporous clubmosses, the heterosporous quillworts, and the heterosporous spikemosses. Each of these has been the focus of several phylogenetic studies (Wikström and Kenrick, 1997; Wikström, 2001; Korall and Kenrick, 2002, 2004; Rydin and Wikström, 2002; Hoot *et al.*, 2006).

Within the euphyllophytes, characterized by euphylls (leaves with marginal or apical meristems and an associated leaf gap in the vascular stele), a deep split subsequently separates seed plants from ferns (Figure 15.1A; Kenrick and Crane, 1997; Doyle, 1998; Nickrent *et al.*, 2000; Renzaglia *et al.*, 2000; Pryer *et al.*, 2001a, 2004a, 2004b; Wikström and Pryer, 2005; Qiu *et al.*, 2006; Schuettpelz *et al.*, 2006). Seed plants, united by the presence of seeds and wood, account for some 96% of extant vascular plant diversity. Accordingly, these plants have received considerable phylogenetic attention (for an overview of relationships, see Burleigh



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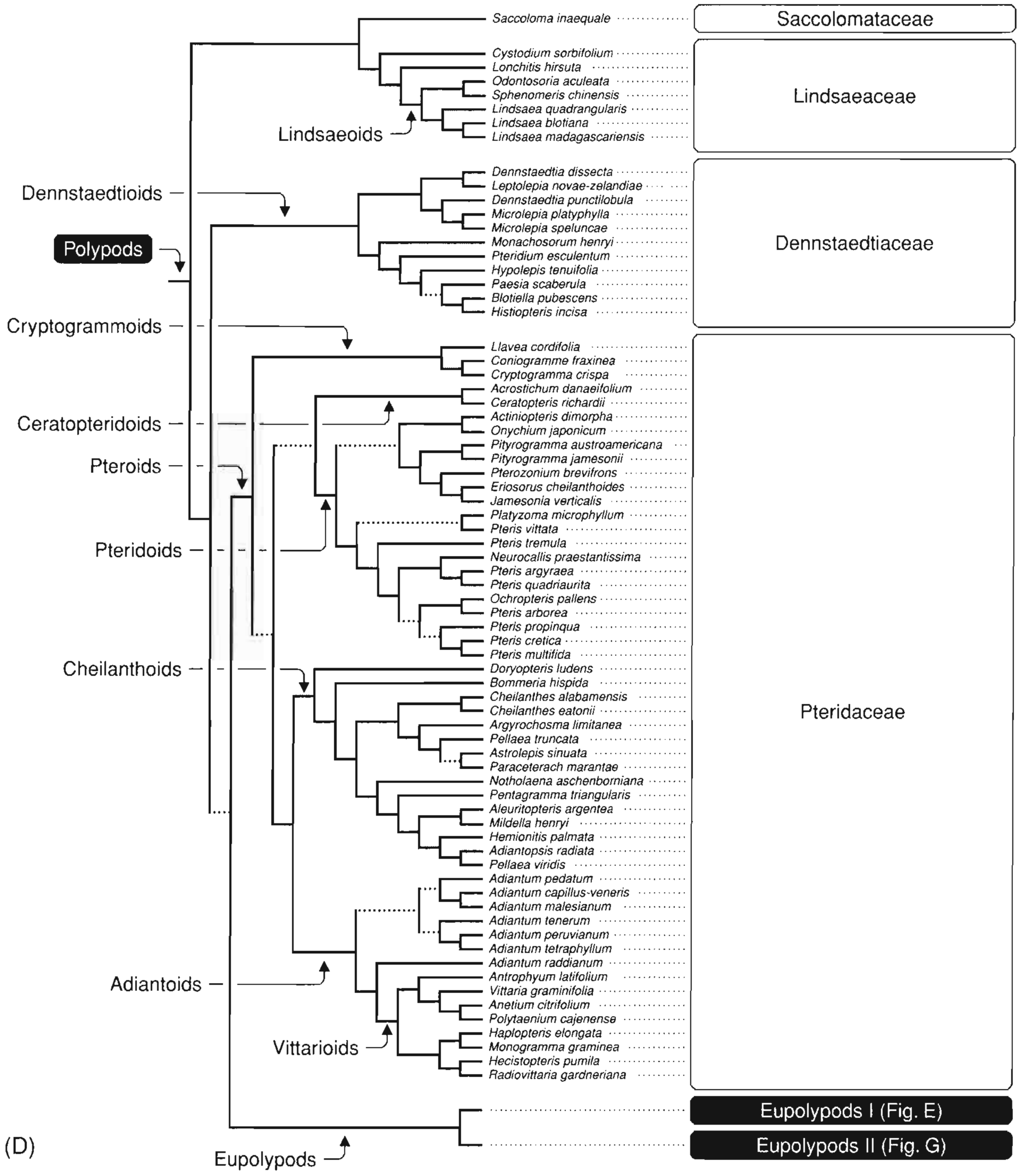
and Mathews, 2004; Soltis and Soltis, 2004). Ferns, while accounting for little more than 3% of vascular plant species, display morphological and ecological disparity rivaling that of their equally ancient sister group. A clear morphological synapomorphy for this clade is lacking. However, ferns are routinely resolved as monophyletic in analyses of morphology (e.g., Renzaglia *et al.*, 2000; Rothwell and Nixon, 2006), and are consistently well supported as a natural group in analyses of DNA sequence data (e.g., Nickrent *et al.*, 2000; Renzaglia *et al.*, 2000; Pryer *et al.*, 2001a, 2004b; Wikström and Pryer, 2005; Qiu *et al.*, 2006; Rothwell and Nixon, 2006; Schuettpelz *et al.*, 2006).

Ferns, like lycophytes, are spore bearing and "seed-free." Because of this, members of these two lineages were traditionally lumped as "pteridophytes" or "ferns and fern allies." Although these terms served the botanical community well when there was little resolution near the base of the vascular plant phylogeny, robustly supported hypotheses resolving these deepest divergences are now available. Thus, "ferns" (in a somewhat more inclusive than traditional sense; see Figure 15.1A) and "lycophytes," which specify clade membership, are



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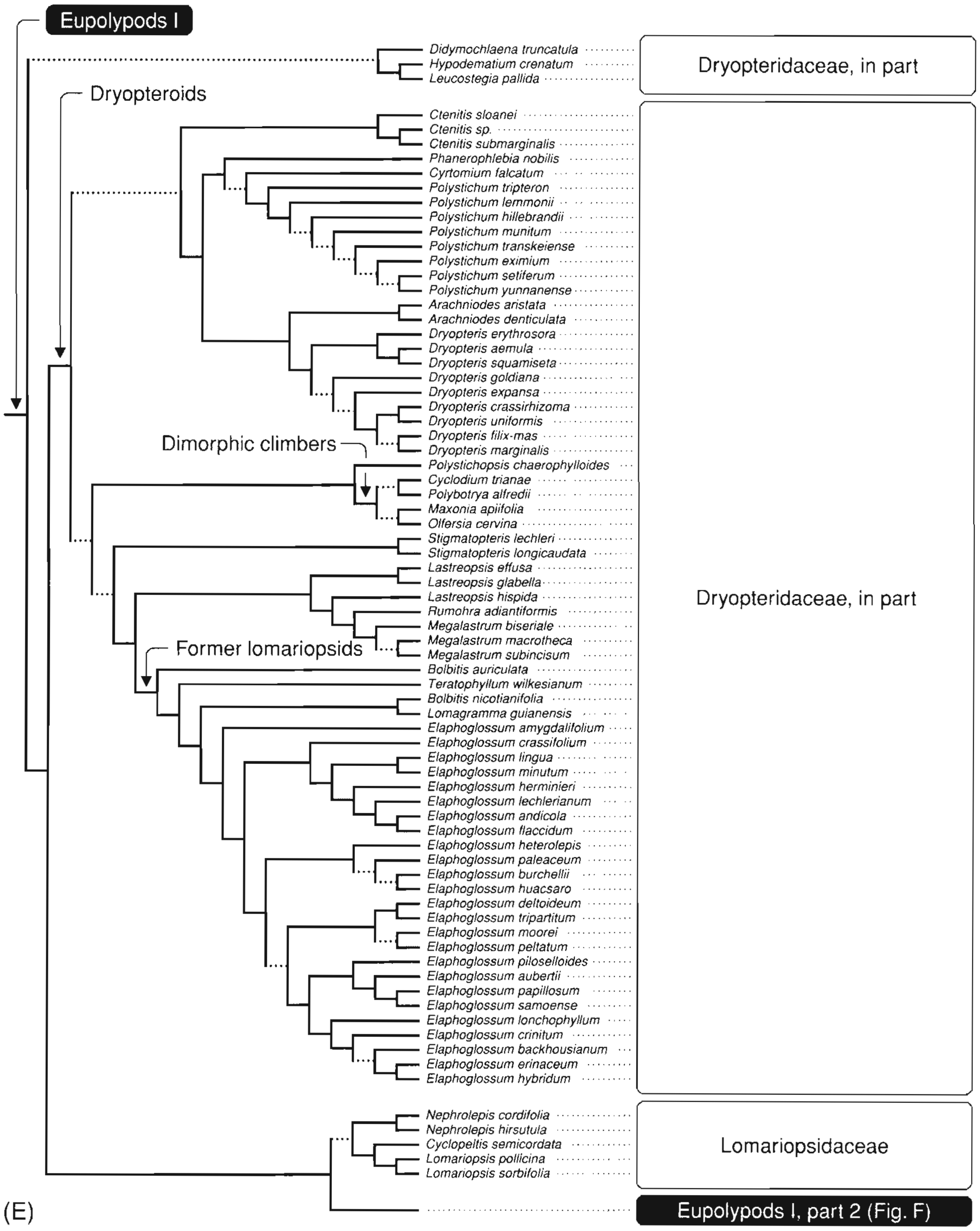
preferable to the terms "pteridophytes" and "ferns and fern allies" that unite paraphyletic assemblages of plants.

15.3 Early fern divergences

Within ferns, the first divergence separates a clade including whisk-ferns and ophioglossoids from a clade including horsetails, marattioids, and leptosporangiates (Figure 15.1A; Nickrent *et al.*, 2000; Pryer *et al.*, 2001a, 2004a, 2004b; Wikström and Pryer, 2005; Qiu *et al.*, 2006; Rothwell and Nixon, 2006;



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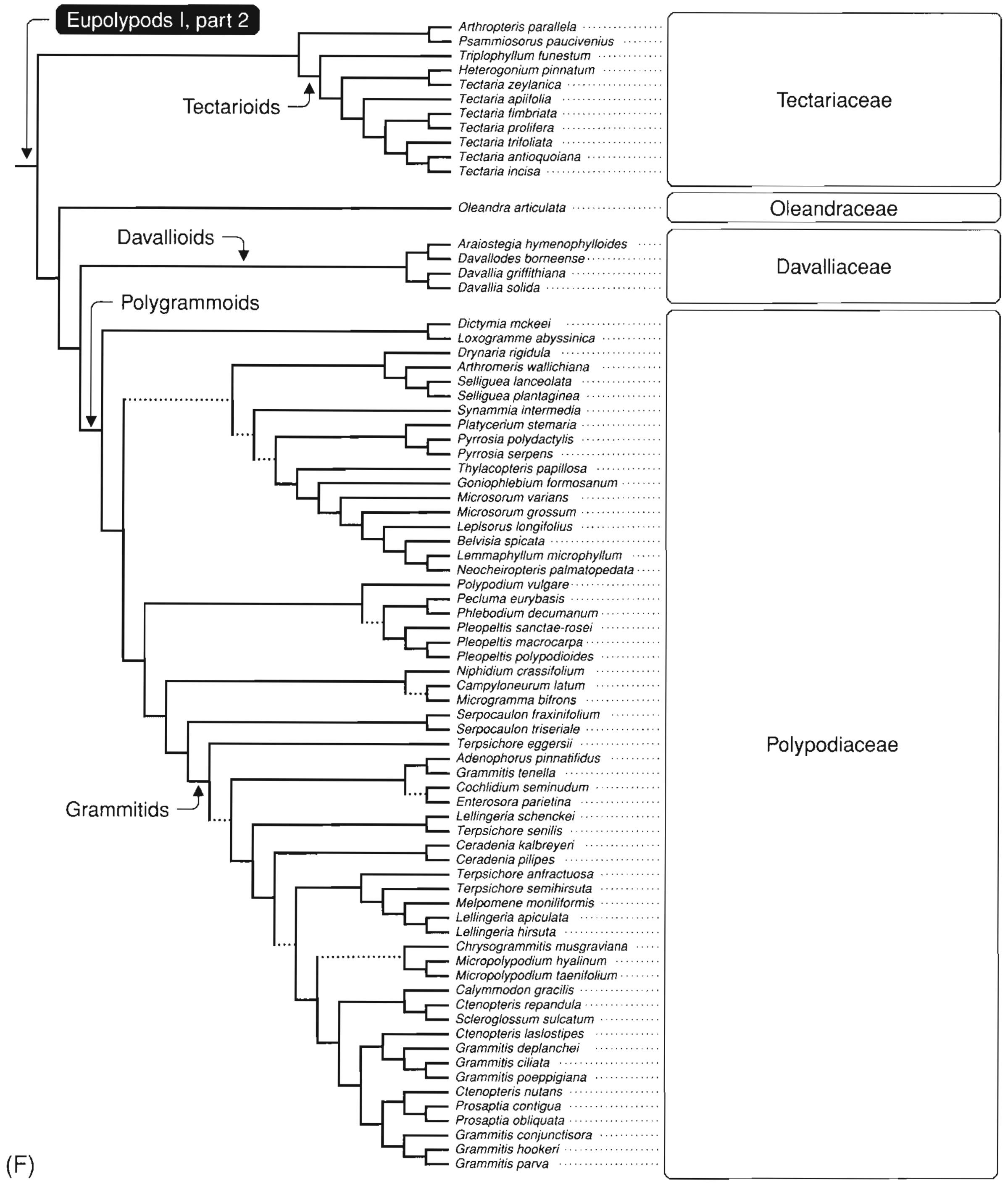
Schuettpelz *et al.*, 2006). Whiskferns (Psilotaceae) and ophioglossoids (Ophioglossaceae) are both relatively small lineages, and both exhibit considerable morphological simplification. Some whiskferns, in fact, have such strikingly simplified body plans that they were long thought to be direct descendants of some of the first vascular plants appearing in the fossil record (Parenti, 1980; Bremer, 1985). This has made unique shared characteristics especially difficult to identify, but reduction of the root system may actually constitute such a trait – ophioglossoids have simple unbranched roots that lack root hairs, and



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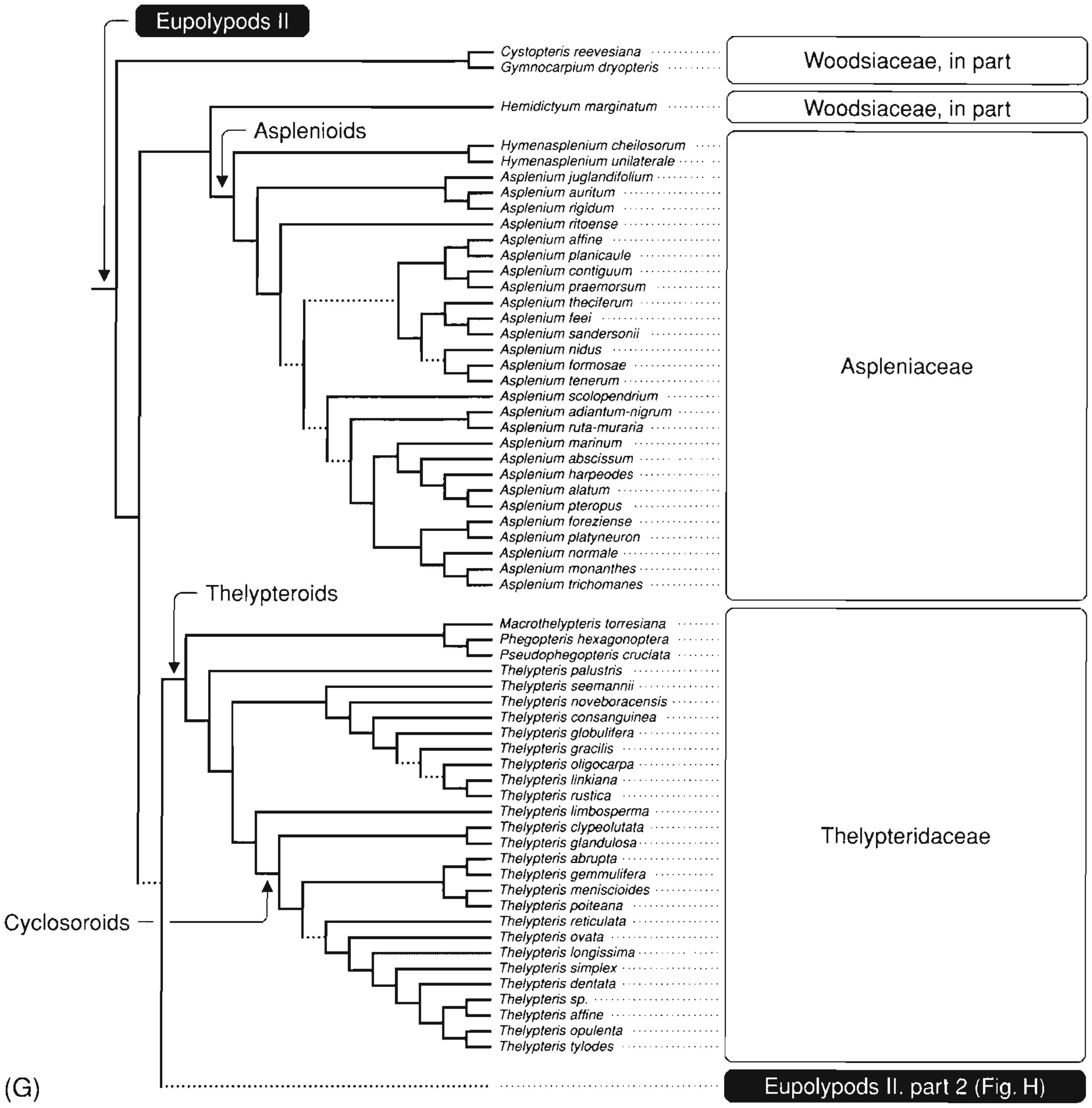
whiskferns lack roots altogether (Schneider *et al.*, 2002a). Phylogenetic studies within this clade have focused primarily on the ophioglossoids (Hauk *et al.*, 2003).

Although well supported together as a clade, the relationships among the horsetail, marattioid, and leptosporangiate lineages remain somewhat elusive (Nickrent *et al.*, 2000; Pryer *et al.*, 2001a, 2004b; Wikström and Pryer, 2005; Qiu *et al.*, 2006; Rothwell and Nixon, 2006; Schuettpelz *et al.*, 2006; see Chapter 13). Their divergence from one another in rather rapid succession deep in time – all arose in the Paleozoic – could be responsible. Horsetails today account for



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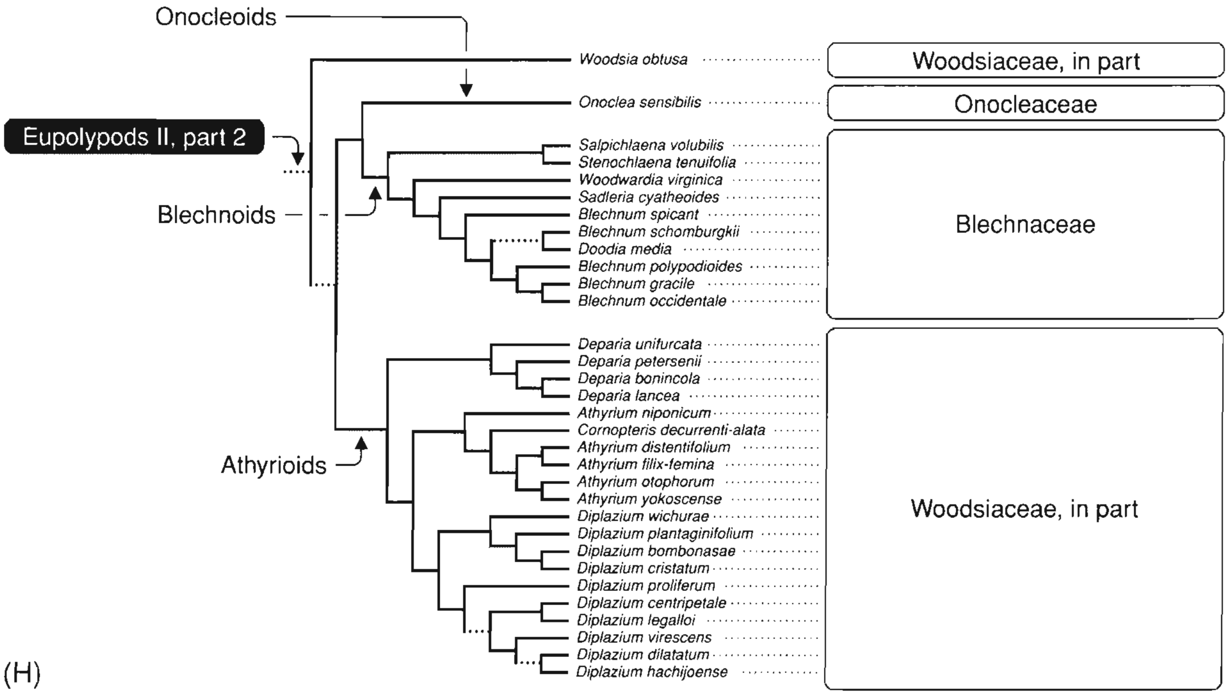
just a handful of species (in a single family, Equisetaceae), apparently resulting from a Cenozoic diversification (Des Marais *et al.*, 2003). The marattioids (Marattiaceae) are somewhat more species rich, but their diversity pales in comparison to the leptosporangiates, which account for well over 95% of extant fern diversity. Leptosporangiates compose a well-supported monophyletic group (Pryer *et al.*, 2001a, 2004b; Schneider *et al.*, 2004c; Wikström and Pryer, 2005; Qiu *et al.*, 2006; Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007) characterized by sporangia that develop from a single cell, have mature walls just one cell thick, and possess a distinctive annulus that serves to eject the spores. Specific features of the sporangia – including the shape and position of the annulus – have figured prominently in the classification of these ferns, and are generally consistent with their phylogeny (see below).



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15.4 Early leptosporangiate divergences

The osmundaceous ferns are well supported as sister to all other leptosporangiates (Figure 15.1B; Pryer *et al.*, 2001a, 2004b; Schneider *et al.*, 2004c; Wikström and Pryer, 2005; Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007), a position consistent with the fossil record because the oldest leptosporangiate fossils assignable to an extant lineage are members of this clade (Miller, 1971; Tidwell and Ash, 1994; Phipps *et al.*, 1998; Galtier *et al.*, 2001; Rößler and Galtier, 2002). These ferns are placed in a single family, Osmundaceae (Figure 15.1B; Smith *et al.*, 2006b; Chapter 16), and are generally divided into three genera. But although recent studies have confirmed the monophyly of *Leptopteris* and *Todea*, they have found strong support for the paraphyly of *Osmunda*; *Osmunda cinnamomea* is resolved sister to the remaining osmundaceous ferns, advocating the recognition of a fourth genus (*Osmundastrum*; Yatabe *et al.*, 1999; Metzgar *et al.*, in press).

The filmy ferns, composing a single large family (Hymenophyllaceae) and the gleichenioid ferns, with three smaller families (Dipteridaceae, Matoniaceae, and Gleicheniaceae) are both now understood to be monophyletic (Figure 15.1B; Pryer *et al.*, 2004b; Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007). However, the relationships of these two lineages to one another and to the remaining leptosporangiate ferns remain unclear. Within filmy ferns, two clades of roughly equal size are resolved (Figure 15.1B; Pryer *et al.*, 2001b; Schuettpelz and Pryer, 2006) – the hymenophylloid clade with a single genus (*Hymenophyllum*) and the trichomanoid clade with eight genera (*Abrodictyum*, *Callistopteris*, *Cephalomanes*, *Crepidomanes*, *Didymoglossum*, *Polyphlebium*, *Trichomanes*, and *Vandenboschia*; Ebihara *et al.*, 2006). Each of these two large filmy fern clades has been the subject of several focused phylogenetic studies (Ebihara *et al.*, 2002, 2004; Dubuisson *et al.*, 2003; Hennequin *et al.*, 2003, 2006a, 2006b); however, because most of these analyses relied on a single gene, relationships were sometimes unsupported. A three-gene analysis (Schuettpelz and Pryer, 2007) still does not find strong support within the epiphytic genus *Hymenophyllum*, but does find good support for relationships among the trichomanoid genera (Figure 15.1B). Two large trichomanoid subclades emerge, one of which is mostly terrestrial (*Abrodictyum*, *Cephalomanes*, and *Trichomanes*), the other of which is mostly epiphytic (*Crepidomanes*, *Didymoglossum*, *Polyphlebium*, and *Vandenboschia*).

Strong support for the monophyly of the gleichenioid ferns (Figure 15.1B) has only recently been obtained (Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007), although earlier morphological (Jarrett, 1980) and molecular (Hasebe *et al.*, 1995; Pryer *et al.*, 2004b) data suggested such a clade. Within gleichenioids, Dipteridaceae is sister to Matoniaceae and these together are sister to the Gleicheniaceae (Figure 15.1B; Schuettpelz and Pryer, 2007).

The schizaeoid ferns are well supported as sister to the so-called "core leptosporangiates" – a large clade composed of heterosporous, tree, and polypod ferns (Figures 15.1B, C; Pryer *et al.*, 2004b; Schuettpelz and Pryer, 2007). The schizaeoids comprise three morphologically and molecularly distinct clades (Figure 15.1B; Skog *et al.*, 2002; Wikström *et al.*, 2002), recognized as distinct families in the most recent fern classification (Lygodiaceae, Schizaeaceae, and Anemiaceae; Smith *et al.*, 2006b; Chapter 16).

The heterosporous, or water, ferns are also monophyletic and comprise two major clades (Figure 15.1C; Hasebe *et al.*, 1995; Pryer *et al.*, 2004b), treated as families (Smith *et al.*, 2006b). The Salviniaceae consists of two free-floating genera: *Azolla* and *Salvinia*. The Marsileaceae consists of three genera, all of which are rooted in the soil: *Marsilea*, *Pilularia*, and *Regnellidium*. These ferns have been the focus of several recent and ongoing phylogenetic studies that have addressed their relationships in greater detail (Pryer, 1999; Reid *et al.*, 2006; Metzgar *et al.*, 2007; Nagalingum *et al.*, 2007).

The tree ferns are well supported as monophyletic in molecular analyses (Pryer *et al.*, 2001a; 2004b; Wikström and Pryer, 2005; Korall *et al.*, 2006b; Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007), but lack an obvious morphological synapomorphy. Many species do indeed have trunk-like stems, but this character is not ubiquitous throughout the clade. The phylogeny of these ferns was specifically examined by Korall *et al.* (2006b), and the phylogenetic branching pattern presented here (Figure 15.1C; Schuettpelz and Pryer, 2007) is in agreement with these results. The Culcitaceae, Loxomataceae, Plagiogyriaceae, and Thyrsopteridaceae together form a clade, as do the Cibotiaceae, Cyatheaceae, Dicksoniaceae, and Metaxyaceae. Within the large scaly tree fern clade (Figure 15.1C; note that this clade is equivalent to Cyatheaceae), four primary subclades emerge: *Sphaeropteris*, *Cyathea* (with *Hymenophyllopsis* embedded within it), and two distinct *Alsophila* clades (Korall *et al.*, 2007; but see Conant *et al.*, 1995, 1996).

Although not always thought to form a natural group, the polypod ferns (Figures 15.1D–H), have received solid support in all recent analyses (Pryer *et al.*, 2001a, 2004b; Schneider *et al.*, 2004c; Wikström and Pryer, 2005; Schuettpelz *et al.*, 2006; Schuettpelz and Pryer, 2007). This clade is united by an unequivocal morphological synapomophy – sporangia each with a vertical annulus interrupted by the stalk.

15.5 Early polypod divergences

The much smaller of the two clades arising from the first divergence within the polypods contains the lindsaeoid ferns and a few rather enigmatic fern genera (Figure 15.1D). Two of the smaller genera (*Lonchitis* and *Saccoloma*) were traditionally placed in the Dennstaedtiaceae; the other (*Cystodium*) was traditionally placed in the Dicksoniaceae, a tree fern family. In the most recent and comprehensive analysis (Schuettpelz and Pryer, 2007), these three genera and the lindsaeoids together form a well-supported clade, but one that was not recovered, in its entirety, in earlier analyses (Hasebe *et al.*, 1995; Pryer *et al.*, 2004b; Schneider *et al.*, 2004c; Korall *et al.*, 2006a; Schuettpelz *et al.*, 2006). In the most recent classification (Smith *et al.*, 2006b; Chapter 16), this clade is divided into two families – Saccolomataceae and Lindsaeaceae. The former comprises only the genus *Saccoloma*; the latter includes eight genera (note that *Ormoloma*, *Tapeinidium*, and *Xyropteris* do not appear in Figure 15.1D).

The remaining polypods compose three well-supported clades: the small dennstaedtioid clade, the large pteroid clade, and the hyperdiverse eupolypod fern clade (Figure 15.1D; Schneider *et al.*, 2004c; Schuettpelz and Pryer, 2007). But again, the relationships among these three lineages remain unclear. Within the dennstaedtioids, two approximately equally diverse subclades are resolved; the genus *Dennstaedtia* itself is strongly supported as paraphyletic (Wolf *et al.*, 1994; Wolf, 1995; Schuettpelz and Pryer, 2007).

The pteroid ferns account for roughly 10% of extant fern diversity, placed in a single family (Pteridaceae; Smith *et al.*, 2006b; Chapter 16). Five primary clades are resolved in molecular phylogenetic analyses (Prado *et al.*, 2007; Schuettpelz *et al.*, 2007; Schuettpelz and Pryer, 2007): cryptogrammoids, ceratopteridoids, pteridoids, cheilanthoids, and adiantoids (with the vittarioid ferns apparently embedded within the genus *Adiantum*; Figure 15.1D). Some finer-scale relationships within most of these groups were addressed in earlier studies (Crane *et al.*, 1995; Gastony and Rollo, 1995, 1998; Nakazato and Gastony, 2003; Sánchez-Baracaldo, 2004; Zhang *et al.*, 2005).

Within the eupolypod ferns, two large clades are resolved, dubbed "eupolypods I" and "eupolypods II" (Figure 15.1D; Schneider *et al.*, 2004c; Schuettpelz and Pryer, 2007). This split is well supported by molecular data, but also by a frequently overlooked morphological character, namely the vasculature of the petiole. Eupolypods I have three or more vascular bundles (with the exception of the diminutive grammitid ferns with one, and the genus *Hypodematium* with two); whereas eupolypods II have only two (with the exception of the well-nested blechnoid ferns with three or more).

15.6 Divergences within eupolypods I

Three genera not traditionally thought to be closely related to one another (*Didymochlaena*, *Hypodematium*, and *Leucostegia*) form a small, but poorly supported clade sister to the rest of eupolypods I (Figure 15.1E). In earlier classifications (e.g., Kramer, 1990a; Kramer *et al.*, 1990), *Didymochlaena* was considered to be associated with the dryopteroid ferns (Figure 15.1E), *Hypodematium* with the athyrioid ferns (Figure 15.1H), and *Leucostegia* among the davallioid ferns (Figure 15.1F). Previous studies found these genera to be rather isolated (Hasebe *et al.*, 1995; Schneider *et al.*, 2004c; Tsutsumi and Kato, 2006), but all three were only recently included in the same analysis (Schuettpelz and Pryer, 2007). The finding of good support for the monophyly of the remaining eupolypods I – excluding *Didymochlaena*, *Hypodematium*, and *Leucostegia* – is the first convincing evidence that these three genera should indeed be segregated from the Dryopteridaceae (Smith *et al.*, 2006b), as they render it paraphyletic (Figure 15.1E).

The dryopteroid ferns form a very large and well-supported clade, with most "former lomariopsid" genera nested within it (Figure 15.1E; Schuettpelz and Pryer, 2007). Notably absent from the dryopteroid clade, however, is the genus *Lomariopsis* itself, which is resolved elsewhere in the eupolypods I (Figure 15.1E). This suggests that the distinctive rhizome anatomy (elongated ventral meristele) characteristic of lomariopsid ferns has apparently evolved at least twice (once in the Dryopteridaceae and once in the Lomariopsidaceae). Within dryopteroids, the well-studied genera *Dryopteris* (Geiger and Ranker, 2005; Li and Lu, 2006) and *Polystichum* (Little and Barrington, 2003; Li *et al.*, 2004) compose a large, well-supported clade together with *Phanerophlebia*, *Cyrtomium*, and *Arachniodes* (Figure 15.1E; Schuettpelz and Pryer, 2007). The genus *Polystichopsis* – which is often synonymized under *Arachniodes* (e.g., Kramer *et al.*, 1990) – is, however, not closely related. Rather, it is sister to a clade of "dimorphic climbers" – dryopteroid genera with creeping (to climbing) stems and dimorphic leaves (Figure 15.1E). *Stigmatopteris*, as well as *Ctenitis*, are both rather isolated, but *Megalastrum* (a relatively recent segregate of *Ctenitis*; Holttum, 1986) forms a clade with *Rumohra* and the paraphyletic genus *Lastreopsis*. This clade is in turn sister to the "former lomariopsid" genera (Figure 15.1E), within which *Bolbitis* is resolved as polyphyletic. *Elaphoglossum*, the largest of the "former lomariopsid" genera is clearly monophyletic (Figure 15.1E), and has received considerable phylogenetic attention (Rouhan *et al.*, 2004; Skog *et al.*, 2004).

Nephrolepis, *Cyclopeltis*, and *Lomariopsis* also form a clade within the eupolypods I, (Figure 15.1E; Tsutsumi and Kato, 2006; Schuettpelz and Pryer, 2007). Although this assemblage is generally not well supported in analyses of molecular data, its monophyly is reinforced by a morphological synapomorphy – specifically the presence of articulate pinnae (Smith *et al.*, 2006b). Oleandroid ferns, on the other hand, which were thought to compose a natural group based on morphology (Kramer, 1990b), are resolved in molecular analyses as definitively not monophyletic (Schuettpelz and Pryer, 2007). Two oleandroid genera (*Arthropteris* and *Psammiosorus*) are sister to the tectarioid ferns (Figure 15.1F); they are now included in the Tectariaceae (Smith *et al.*, 2006b). *Oleandra* itself is sister to a large clade of davallioid and polygrammoid ferns (Figure 15.1F), and is now considered to be the sole genus in Oleandraceae (Smith *et al.*, 2006b).

The phylogeny of davallioid and polygrammoid ferns has been extremely well studied in recent years (Schneider *et al.*, 2002b, 2004a, 2004d, 2006a, 2006b; Haufler *et al.*, 2003, Ranker *et al.*, 2003, 2004; Janssen and Schneider, 2005; Tsutsumi and Kato, 2005, 2006; Kreier and Schneider, 2006a, 2006b), and the relationships presented (Figure 15.1F) are generally consistent with those resolved in earlier studies. As previously determined, the grammitid ferns (Grammitidaceae *sensu* Parris, 1990) are nested firmly within the Polypodiaceae *sensu* Hennipman *et al.* (1990). There is now strong support for the newly described genus *Serpocaulon* (Smith *et al.*, 2006a) as sister to the grammitid clade (Figure 15.1F; Schuettpelz and Pryer, 2007).

15.7 Divergences within eupolypods II

Eupolypods II consists of several large well-supported clades with a number of small genera interspersed among them. Among the smaller genera, *Cystopteris* and *Gymnocarpium* are notable in being sister to the rest of eupolypods II; *Hemidictyum* is sister to the large asplenioid clade; and *Woodsia* is sister to the onocleoid, blechnoid, and athyrioid ferns (Figure 15.1G, H; Schuettpelz and

Pryer, 2007). All four of these genera were tentatively placed in the Woodsiaceae (Smith *et al.*, 2006b); however, it seems that this circumscription is paraphyletic, relative to the other families in the eupolypods II, and in need of further study.

The asplenioid ferns (Figure 15.1G) are among the larger eupolypods II clades that have consistently received strong support in molecular analyses (Gastony and Johnson, 2001; Schuettpelz and Pryer, 2007). Earlier studies have clearly demonstrated that nearly all genera previously segregated from *Asplenium* (e.g., *Camptosorus*, *Diellia*, and *Loxoscaphe*) nest well within this large genus (Murakami and Schaal, 1994; Murakami *et al.*, 1999; Pinter *et al.*, 2002; Schneider *et al.*, 2004b, 2005; Perrie and Brownsey, 2005). Thus, in the most recent classification (Smith *et al.*, 2006b; Chapter 16) only two genera were recognized in the Aspleniaceae, *Hymenasplenium* being sister to *Asplenium* (Figure 15.1G).

The thelypteroid ferns are also strongly supported as monophyletic (Figure 15.1G; Smith and Cranfill, 2002; Schuettpelz and Pryer, 2007) and are recognized as a large family (Thelypteridaceae) with five genera (Smith *et al.*, 2006b). The three smaller genera (*Macrothelypteris*, *Phegopteris*, and *Pseudophegopteris*) form a clade sister to the two larger genera (*Cyclosorus* and *Thelypteris*; Figure 15.1G; Smith and Cranfill, 2002; Schuettpelz and Pryer, 2007). *Thelypteris* (*sensu* Smith, 1990) is, however, definitively paraphyletic to the cyclosoroids (Figure 15.1G; note that all species potentially assignable to *Cyclosorus* are presented in Figure 15.1G under *Thelypteris* to circumvent a variety of nomenclatural issues). The thelypteroid clade is in need of considerable phylogenetic study.

The onocleoid ferns, including *Onoclea* (and three other small genera not appearing in Figure 15.1H; Gastony and Ungerer, 1997; Smith *et al.*, 2006b), are sister to a larger blechnoid clade that was the subject of three recent studies (Nakahira, 2000; Cranfill, 2001; Cranfill and Kato, 2003). The results presented here (from Schuettpelz and Pryer, 2007) are in general accord with their more densely sampled analyses: *Blechnum* is definitely not monophyletic (Figure 15.1H) and blechnoid taxonomy thus requires further attention.

The athyrioid ferns, which account for most of the diversity in the paraphyletic Woodsiaceae, are themselves monophyletic (Figure 15.1H; Schuettpelz and Pryer, 2007). However, the largest genera in this clade, *Athyrium* and *Diplazium*, are likely not (see Sano *et al.*, 2000; Wang *et al.*, 2003; not entirely evident in Figure 15.1G).

15.8 Future prospects

DNA sequence data and phylogenetic approaches have revolutionized fern systematics, providing an unparalleled framework within which to explore evolutionary patterns. However, many questions remain at every scale, and the inclusion of many more taxa and additional data will be required to ultimately bring the fern tree of life into focus. Only with a continued effort to improve our understanding of phylogeny will a full appreciation of fern, as well as lycophyte, evolution and diversification be possible.

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