

# Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes

Eric Schuettpelez & Kathleen M. Pryer

*Department of Biology, Duke University, Durham, North Carolina 27708, U.S.A. ejs7@duke.edu (author for correspondence)*

In an effort to obtain a solid and balanced approximation of global fern phylogeny to serve as a tool for addressing large-scale evolutionary questions, we assembled and analyzed the most inclusive molecular dataset for leptosporangiate ferns to date. Three plastid genes (*rbcL*, *atpB*, *atpA*), totaling more than 4,000 bp, were sequenced for each of 400 leptosporangiate fern species (selected using a proportional sampling approach) and five outgroups. Maximum likelihood analysis of these data yielded an especially robust phylogeny: 80% of the nodes were supported by a maximum likelihood bootstrap percentage  $\geq 70$ . The scope of our analysis provides unprecedented insight into overall fern relationships, not only delivering additional support for the deepest leptosporangiate divergences, but also uncovering the composition of more recently emerging clades and their relationships to one another.

**KEYWORDS:** eupolypods, leptosporangiates, molecular systematics, monilophytes, phylogenetics, polypods, tree of life

## INTRODUCTION

An accurate and robust assessment of phylogeny is fundamental to a full understanding of evolutionary origins because it provides the overall pattern of historical divergence—a framework for exploring both evolution and diversification. Although reconstructing phylogeny remains a challenging endeavor, the use of DNA sequence data has revolutionized our ability to assess relationships in many groups, including leptosporangiate ferns, a large well-supported clade of vascular plants (Pryer & al., 2001a, 2004) characterized by sporangia that develop from a single cell and have mature walls just one cell thick.

Molecular phylogenetic analyses including representative placeholder taxa have revealed the composition of, and the relationships among, the major leptosporangiate lineages (Hasebe & al., 1993, 1994, 1995; Pryer & al., 1995, 2001a, 2004; Wolf, 1996, 1997; Vangerow & al., 1999; Schneider & al., 2004c; Wikström & Pryer, 2005; Schuettpelez & al., 2006). Densely sampled analyses within some of these groups have elucidated more detailed associations and have provided a phylogenetic framework for more narrowly-focused evolutionary studies (see references cited under various taxonomic groups in Discussion). However, neither placeholder sampling from various clades nor dense sampling within a particular clade is well suited to addressing large-scale evolutionary questions across leptosporangiate ferns. A more comprehensive approach is necessary.

The most inclusive analysis of leptosporangiate fern relationships conducted to date was the groundbreaking

collaborative study of Hasebe & al. (1995). Although this study helped answer many long-standing questions in fern systematics (Smith, 1995), it was not without problems. With about 9,000 extant species in 267 genera (Smith & al., 2006b), leptosporangiate ferns are, after angiosperms, the most diverse lineage of vascular plants. Yet, the Hasebe & al. (1995) study sampled just 99 species from 92 genera, excluding almost two thirds of leptosporangiate fern genera and undersampling all but the smallest. Furthermore, it was founded on a single plastid gene (1,206 base pairs of *rbcL*), resulting in relatively low levels of branch support across the phylogeny (only about half of the resolved nodes were supported by maximum parsimony or neighbor joining bootstrap percentages  $\geq 70$ ).

To obtain a better-sampled and better-supported estimate of overall fern relationships and move one step closer to a comprehensive phylogeny of extant ferns, a considerably larger dataset is assembled and analyzed here. It comprises 400 leptosporangiate species from 187 genera—well over 4% of the species and more than two-thirds of the genera (Smith & al., 2006b)—sampled in proportion to lineage size, to provide a more accurate and balanced representation of the fern tree of life. For each species, three plastid protein-coding genes were sequenced—totaling more than 4,000 base pairs—to ensure a well-supported phylogeny. The current analysis builds upon the foundation of earlier studies to provide an unparalleled framework within which to examine the evolution and diversification of leptosporangiate ferns, while simultaneously improving our phylogenetic understanding of this important lineage.

## MATERIALS AND METHODS

**Taxonomic sampling.** — In phylogenetic studies, a strict placeholder approach is often utilized (i.e., a single species is used to represent each genus in intrafamilial studies, a single genus is used to represent each family in intraordinal studies, etc.). While such an approach is appropriate when the goal is to simply infer evolutionary relationships at a given level, it does not provide a balanced representation of phylogeny. Exhaustive sampling would be the ideal solution, but this is still not feasible for broad analyses. Therefore, in this study, an alternative hybrid approach is employed. An attempt is made to sample lineages (i.e., families and genera) in proportion to the number of species they contain. In total, 400 leptosporangiate fern species were selected from all families recognized in the most recent phylogeny-based classification for ferns (Smith & al., 2006b); all large genera and many small genera are included (Appendix 1 in Electronic supplement). To root the leptosporangiate phylogeny, five outgroup species were selected from the most closely related eusporangiate clades, namely horsetail and marattioid ferns (Pryer & al., 2001a, 2004; Schuettpeitz & al., 2006; Wikström & Pryer, 2005).

### DNA isolation, amplification, and sequencing.

— Due to the scale of this study, there was some variation in the protocol used to obtain new DNA sequences for analysis. However, deviations from the general protocol described here were minimal and generally insignificant.

Genomic DNA was extracted from silica-dried material using the DNeasy Plant Mini Kit (Qiagen). Dry leaf tissue ( $\leq 20$  mg) was sealed in a microcentrifuge tube with approximately fifty 0.7 mm zirconia beads (BioSpec Products) and frozen in liquid nitrogen. After 10 minutes, the sealed tubes were removed from the liquid nitrogen, placed in a Mini-BeadBeater-8 (BioSpec Products), and “beaten” for 10 sec at maximum speed. Lysis buffer and RNase were added directly to the tube (beads were not removed) and the tubes were incubated at 65°C for 30 min. Extraction then proceeded following the manufacturer’s protocol, including the recommended 5 min lysate centrifugation and performing two 50  $\mu$ l elutions into the same microcentrifuge tube.

For each species, three protein-coding plastid genes (*rbcL*, *atpB*, *atpA*) were separately amplified using the polymerase chain reaction (PCR). Each 25  $\mu$ l reaction incorporated 1X PCR buffer IV containing MgCl<sub>2</sub> (AB-gene), 200  $\mu$ M each dNTP, 100  $\mu$ g/ml BSA, 50 U/ml Taq polymerase, 0.5  $\mu$ M each primer (see Appendix 2 in Electronic supplement, for amplification primers used routinely for each gene), and 1  $\mu$ l template DNA eluate. For *rbcL* and *atpB* amplifications, thermocycling programs entailed an initial denaturation step (94°C for 5 min) followed by 35 denaturation, annealing, and elon-

gation cycles (94°C for 1 min, 45°C for 1 min, 72°C for 2 min) and a final elongation step (72°C for 10 min). For *atpA* amplifications, cycle elongations were increased to 3 min. PCR products were purified using Montage PCR Centrifugal Filter Devices (Millipore).

Sequencing of the cleaned PCR products employed the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Each 10  $\mu$ l reaction incorporated 0.375X BigDye Terminator Ready Reaction Mix (Applied Biosystems), 0.625X BigDye Terminator Sequencing Buffer (Applied Biosystems), 1  $\mu$ M primer (see Appendix 2 in Electronic supplement, for sequencing primers used routinely for each gene), and 2  $\mu$ l purified PCR product. Thermocycling and purification followed the manufacturer’s protocol. Sample electrophoresis and analysis were performed using an ABI Prism 3700 DNA Analyzer (Applied Biosystems). The multiple sequencing reads obtained as chromatograms from each individual purified PCR product (i.e., the reads obtained from each gene, from each species) were assembled and edited separately using Sequencher 4.5 (Gene Codes Corporation). All consensus sequences (784 newly obtained) were subsequently deposited in GenBank (Appendix 1 in Electronic supplement).

### Sequence alignment and phylogenetic analysis.

— The consensus sequences for each gene were manually aligned using MacClade 4.08 (Maddison & Maddison, 2005). The extreme 5' and 3' ends of the *rbcL* and *atpB* alignments containing copious amounts of missing data were removed, as were the unalignable non-coding regions amplified with the *atpA* gene (Schuettpeitz & al., 2006) and the terminal 5' and 3' ends of the *atpA* gene itself.

The three single-gene datasets and the combined three-gene dataset were phylogenetically analyzed using RAxML-VI-HPC 2.2.1 (Randomized Axelerated Maximum Likelihood for High Performance Computing; Stamatakis, 2006). All analyses utilized the GTRMIX model of nucleotide substitution and the rapid hill-climbing algorithm; in the combined analysis, model parameters were estimated and optimized separately for each gene. Each analysis comprised 1,000 alternative runs from distinct randomized maximum parsimony starting trees. To assess branch support, non-parametric bootstrap analyses (with 1,000 replicates) were conducted using RAxML-VI-HPC.

## RESULTS

**Single-gene datasets.** — The portions of the *rbcL*, *atpB*, and *atpA* genes analyzed in this study comprised 1,308, 1,278, and 1,506 bp respectively (Table 1). All three of these datasets were essentially complete, but there was some variation in their information content. The *atpA*

dataset contained a considerably greater number—and a slightly higher percentage—of variable characters than the *rbcL* dataset, which in turn offered an improvement over the *atpB* dataset.

Maximum likelihood analyses of the three single-gene datasets resulted in largely congruent topologies (trees not presented), with conflicting resolutions almost always lacking good bootstrap support (i.e.,  $\geq 70\%$ ; the seven inconsequential exceptions were only marginally well-supported). The differences in phylogenetic signal among the datasets were reflected in the robustness of resolved relationships; the *atpA*, *rbcL*, and *atpB* datasets provided bootstrap support  $\geq 70\%$  for 249, 229, and 222 nodes, respectively (Table 1).

**Combined three-gene dataset.** — The combined dataset comprised 4,092 characters, of which 2,422 were variable. Analysis of these data resulted in a robust assessment of fern relationships (Fig. 1). Of the 402 nodes resolved in the 405-taxon analysis, 322 nodes (80%) were supported by a bootstrap percentage  $\geq 70$  (Table 1).

## DISCUSSION

Although the primary objective of our study was to provide a solid and balanced framework for future analyses of fern evolution and diversification, the resulting phylogeny also fills an important gap in our understanding of fern relationships. To date, the bulk of phylogenetic research in ferns has focused on rather recent divergences, examining evolutionary patterns within specific clades. A few studies have focused on the deepest divergences, uncovering the associations of the most fundamental lineages. What were missing, for the most part, were studies aimed at connecting the dots, determining the composition of more recently emerging clades and their relationships to one another. The scope of our analysis provides such a link, and in the following paragraphs we provide an overview of relationships at this level. In general, we avoid discussion of the finest scale relationships—especially in groups where considerable work has already been conducted. Instead, we direct the reader to the more densely sampled studies. It should be noted that our results, for the most part, have already been incorporated into a modern revision of fern classification (Smith & al., 2006b); therefore, this classification

(followed below) is consistent with our phylogeny, with only a few exceptions.

### Early leptosporangiate divergences (Fig. 1A).

The earliest divergences within the leptosporangiate ferns (labeled “le” in Fig. 1A), as resolved in this study, are in full agreement with those resolved in previous three-gene analyses (Wolf, 1996; Pryer & al., 2001a, 2004; Schneider & al., 2004c; Wikström & Pryer, 2005; Schuettpeitz & al., 2006). The osmundaceous ferns (of, Fig. 1A) are well-supported as sister to all other leptosporangiates (bootstrap support, BS = 100%). This position is consistent with the fossil record because the oldest leptosporangiate fossils assignable to an extant lineage are members of this clade (Miller, 1971; Tidwell & Ash, 1994; Phipps & al., 1998; Galtier & al., 2001; Rößler & Galtier, 2002). Osmundaceous ferns are placed in a single family, Osmundaceae (Osm, Fig. 1A; Smith & al., 2006b). The intrafamilial relationships we resolve—with *Osmunda cinnamomea* sister to *Leptopteris* and *Todea*—are in agreement with more densely-sampled studies (Yatabe & al., 1999; Metzgar & al., in press), although the likely paraphyly of *Osmunda* is not reflected here because only one species was sampled from this relatively small genus.

The filmy ferns (ff), composing a single large family (Hymenophyllaceae; Hym) and the gleichenioid ferns (gl), with three smaller families (Dipteridaceae, Matoniaceae, and Gleicheniaceae; Dip, Mat, and Gle, respectively) are both clearly monophyletic (BS = 100%, 86%, respectively, Fig. 1A). However, the relationships of these lineages to one another and to the remaining leptosporangiate ferns are not well-supported.

Within filmy ferns, two clades of roughly equal size are resolved, in agreement with earlier studies (Pryer & al., 2001b; Schuettpeitz & Pryer, 2006). The hymenophylloid clade (hy, Fig. 1A) contains a single genus—*Hymenophyllum*. The trichomanoid clade (tr, Fig. 1A) comprises eight genera—*Abrodictyum*, *Callistopteris* (not sampled here), *Cephalomanes*, *Crepidomanes*, *Didymoglossum*, *Polyphlebium*, *Trichomanes*, and *Vandenboschia* (Ebihara & al., 2006). Each of these two large filmy fern clades has already been the subject of several more focused phylogenetic studies (Ebihara & al., 2002, 2004, 2006; Dubuisson & al., 2003; Hennequin & al., 2003, 2006a, 2006b); however, because most of these analyses relied on a single gene, relationships were often unsupported. Our three-gene analysis still does not find strong support

**Table 1. Statistics for the four datasets analyzed in this study of leptosporangiate fern phylogeny.**

Dataset	Characters (bp)	Variable characters (bp)	Missing data	Nodes with bootstrap support $\geq 70\%$
<i>rbcL</i>	1,308	784	1.1%	229
<i>atpB</i>	1,278	705	3.2%	222
<i>atpA</i>	1,506	933	0.7%	249
Combined	4,092	2,422	1.6%	322

Leptosporangiates

Phylogram (with branch lengths)

Fam Cladogram (with branch support)

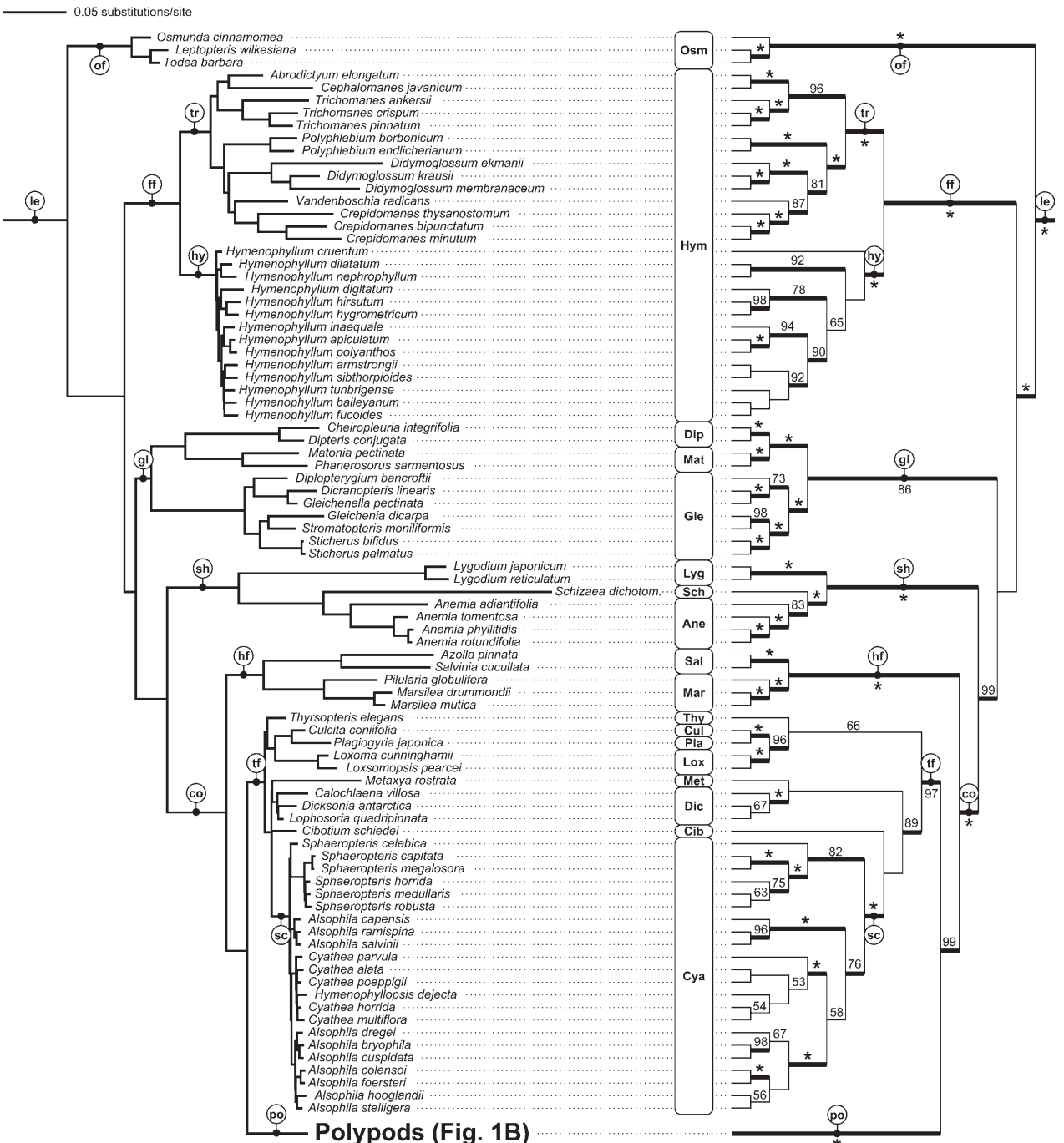


Fig. 1A. Leptosporangiate fern phylogeny resulting from maximum likelihood analysis of plastid *rbcL*, *atpB*, and *atpA* data, presented both as a phylogram (left) to reveal branch lengths and a cladogram (right) to clarify relationships and allow for the presentation of maximum likelihood bootstrap percentages (only percentages  $\geq 50$  are given; if  $\geq 70\%$ , branches are bolded; \* = 100%). Note that the five euposporangiate fern outgroups have been pruned. Major clades discussed in text are indicated in circles on trees: co, core leptosporangiate ferns; ff, filmy ferns; gl, gleichenioids; hf, heterosporous ferns; hy, hymenophylloids; le, leptosporangiate ferns; of, osmundaceous ferns; po, polypods; sc, scaly tree ferns; sh, schizaeoids; tf, tree ferns; tr, trichomanoids. Families recognized in the most recent classification of extant ferns (Smith & al., 2006b) are indicated in boxes between trees: Ane, Anemiaceae; Cib, Cibotiaceae; Cul, Culcitaceae; Cya, Cyatheaceae; Dic, Dicksoniaceae; Dip, Dipteridaceae; Gle, Gleicheniaceae; Hym, Hymenophyllaceae; Lox, Loxomataceae; Lyg, Lygodiaceae; Mar, Marsileaceae; Mat, Matoniaceae; Met, Metaxyaceae; Osm, Osmundaceae; Pla, Plagiogyriaceae; Sal, Salviniaceae; Sch, Schizaeaceae; Thy, Thyrsopteridaceae. Phylogeny continues in Fig. 1B.

within the epiphytic genus *Hymenophyllum*, but we do find good support ( $BS \geq 70\%$ ) for all relationships among the trichomanoid genera (tr, Fig. 1A). From our sampling, 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 (gl, Fig. 1A) has only recently been obtained (Schuettpelz & al., 2006), although earlier morphological (Jarrett, 1980) and molecular (Hasebe & al., 1995; Pryer & al., 2004) data suggested it. Our current analysis corroborates this hypothesis, and also supports the monophyly of each of the three included families ( $BS = 100\%$ , Fig. 1A). Dipteridaceae (Dip) is sister to Matoniaceae (Mat); together, these are sister to the Gleicheniaceae (Gle).

The schizaeoid ferns (sh, Fig. 1A) are well supported ( $BS = 99\%$ ) as sister to the so-called “core leptosporangiates” (co, Fig. 1A; Pryer & al., 2004), a large clade composed of heterosporous (hf), tree (tf), and polypod (po) ferns (Fig. 1A). The schizaeoids are clearly monophyletic ( $BS = 100\%$ ) and compose three morphologically and molecularly distinct families (Fig. 1A): Lygodiaceae (Lyg), Schizaeaceae (Sch), and Anemiaceae (Ane). The relationships resolved here, both among and within these families, are in agreement with earlier analyses (Skog & al., 2002; Wikström & al., 2002).

The heterosporous, or water, ferns (hf, Fig. 1A) comprise two families. The Salviniaceae (Sal) consists of two free-floating genera: *Azolla* and *Salvinia*. The Marsileaceae (Mar) consists of three genera, all of which are rooted in the soil: *Marsilea*, *Pilularia*, and *Regnellidium* (not sampled here). These ferns have been the focus of several recent and ongoing phylogenetic studies that have addressed their relationships in greater detail (Pryer, 1999; Reid & al., 2006; Metzgar & al., 2007; Nagalingum & al., 2007).

The tree ferns (tf, Fig. 1A), are well-supported as monophyletic here ( $BS = 97\%$ ) and in other molecular analyses (Pryer & al., 2001a, 2004; Wikström & Pryer, 2005; Korall & al., 2006b; Schuettpelz & al., 2006), but are lacking 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 recently examined by Korall & al. (2006b), and the branching pattern we recover (Fig. 1A) is in agreement with their results. The Culcitaceae (Cul), Loxomataceae (Lox), Plagiogyriaceae (Pla), and Thyrsopteridaceae (Thy) together form a clade, as do the Cibotiaceae (Cib), Cyatheaceae (Cya), Dicksoniaceae (Dic), and Metaxyaceae (Met). Within the large scaly tree fern clade (sc, Fig. 1A; note that this clade is equivalent to Cyatheaceae), four primary subclades emerge: *Sphaerop-*

*teris*, *Cyathea* (with *Hymenophyllopsis* embedded within it), and two distinct *Alsophila* clades (Korall & al., 2007; but see Conant & al., 1995, 1996).

Although not always thought to form a natural group, the polypod ferns (po, Fig. 1A), have received solid support in all recent analyses (Pryer & al., 2001a, 2004; Schneider & al., 2004c; Wikström & Pryer, 2005; Schuettpelz & al., 2006), and in our analysis as well ( $BS = 100\%$ , Fig. 1A). This clade is united by an unequivocal morphological synapomorphy—sporangia each with a vertical annulus interrupted by the stalk (see Fig. 7C in Pryer & al., 1995).

**Early polypod divergences (Fig. 1B).** — The much smaller of the two clades arising from the first divergence within the polypods contains the lindsaeoid ferns (li, Fig. 1B) and a few rather enigmatic fern genera; two (*Lonchitis* and *Saccoloma*) were traditionally placed in the Dennstaedtiaceae, and one (*Cystodium*) was traditionally placed in the Dicksoniaceae, a tree fern family. In our analysis, these ferns together form a well-supported clade ( $BS = 74\%$ ), but one that has not been recovered, in its entirety, in previous analyses (Wolf & al., 1994; Hasebe & al., 1995; Wolf, 1995; Pryer & al., 2004; Schneider & al., 2004c; Korall & al., 2006a; Schuettpelz & al., 2006). In the most recent classification (Smith & al., 2006b), this clade is divided into two families (Fig. 1B), Saccolomataceae (Sac) and Lindsaeaceae (Lin). The former comprises only the genus *Saccoloma*; the latter includes eight genera (*Ormoloma*, *Tapeinidium*, and *Xyopteris* were not sampled here).

The remaining polypods compose three well-supported clades ( $BS = 100\%$ , Fig. 1B): the small dennstaedtioid clade (de), the large pteroid clade (pt), and the hyperdiverse eupolypod fern clade (eu). Unfortunately, the relationships among these three lineages are unclear. Within the dennstaedtioids (de, Fig. 1B), two approximately equally diverse subclades emerge. This result is in agreement with earlier phylogenetic studies of the group (Wolf & al., 1994; Wolf, 1995). In these studies, and in our analysis, the genus *Dennstaedtia* is strongly supported ( $BS = 100\%$ ) as paraphyletic.

The pteroids (pt) account for roughly 10% of extant fern diversity. In our analysis we resolve five primary clades (Fig. 1B), which is in agreement with a recent molecular phylogenetic study focused specifically on pteroid relationships (Schuettpelz & al., 2007): cryptogrammooids (cr), ceratopteridoids (ce), pteridoids (pd), cheilanthoids (ch), and adiantoids (ad). The vittarioid ferns (vi) are apparently embedded within the genus *Adiantum* ( $BS = 84\%$ ). The finer-scale relationships within most of these groups have already been addressed in earlier studies (Crane & al., 1995; Gastony & Rollo, 1995, 1998; Nakazato & Gastony, 2003; Sánchez-Baracaldo, 2004; Zhang & al., 2005).

**Initial eupolypod divergence (Fig. 1C).** — Within the eupolypod ferns (eu), two large clades are resolved, dubbed “eupolypods I” and “eupolypods II” (Schneider & al., 2004c). This split is well-supported by molecular data (BS = 100%, e1 and e2, Fig. 1C), but also by a frequently overlooked morphological character, namely the vasculature of the petiole. Eupolypods I (e1) have three or more vascular bundles (with the exception of the diminutive grammitid ferns with one, and the genus *Hypodematum*

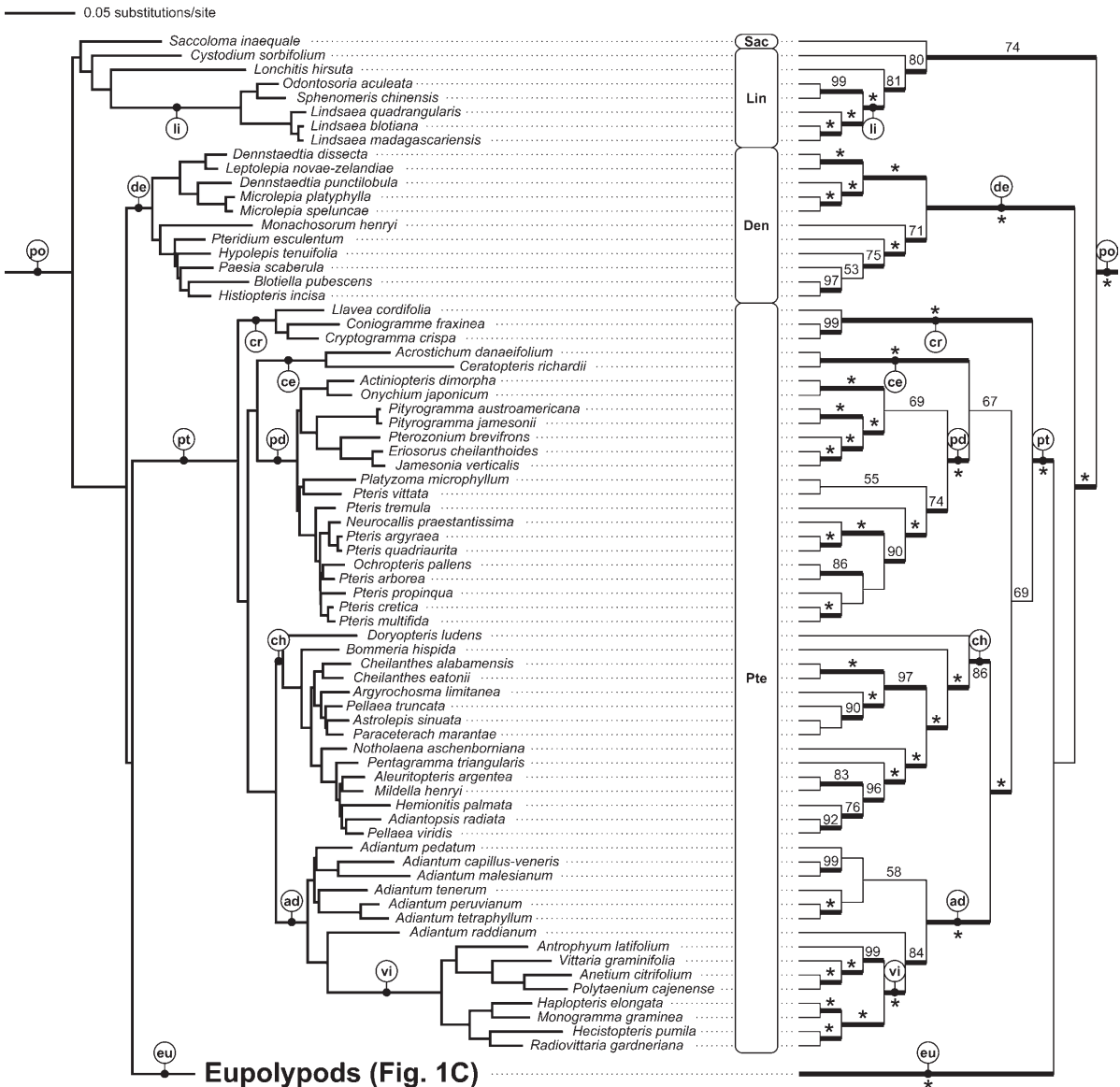
with two); whereas eupolypods II (e2) have only two (with the exception of the well-nested blechnoid ferns with three or more).

**Divergences within eupolypods II (Fig. 1C).** — The eupolypods II (e2) consists of several large well-supported clades with a number of small genera interspersed among them (Fig. 1C). Together, *Cystopteris* and *Gymnocarpium* are sister to the rest of eupolypods II; *Hemidictyum* is sister to the asplenoid ferns (as); and *Woodsia* is sister to a

**Polypods**

**Phylogram (with branch lengths)**

**Cladogram (with branch support)**



**Fig. 1B.** Continued from Fig. 1A. Major clades discussed in text are indicated in circles on trees: ad, adiantoids; ce, ceratopteridoids; ch, cheilanthoids; cr, cryptogrammoid; de, dennstaedtioids; eu, eupolypods; li, lindsaeoids; pd, pteridoids; po, polypods; pt, pteroids; vi, vittarioids. Families recognized in the most recent classification of extant ferns (Smith & al., 2006b) are indicated in boxes between trees: Den, Dennstaedtiaceae; Lin, Lindsaeaceae; Pte, Pteridaceae; Sac, Saccolomataceae. Phylogeny continues in Fig. 1C.

### Eupolypods

Phylogram (with branch lengths) ..... **Fam** ..... Cladogram (with branch support)

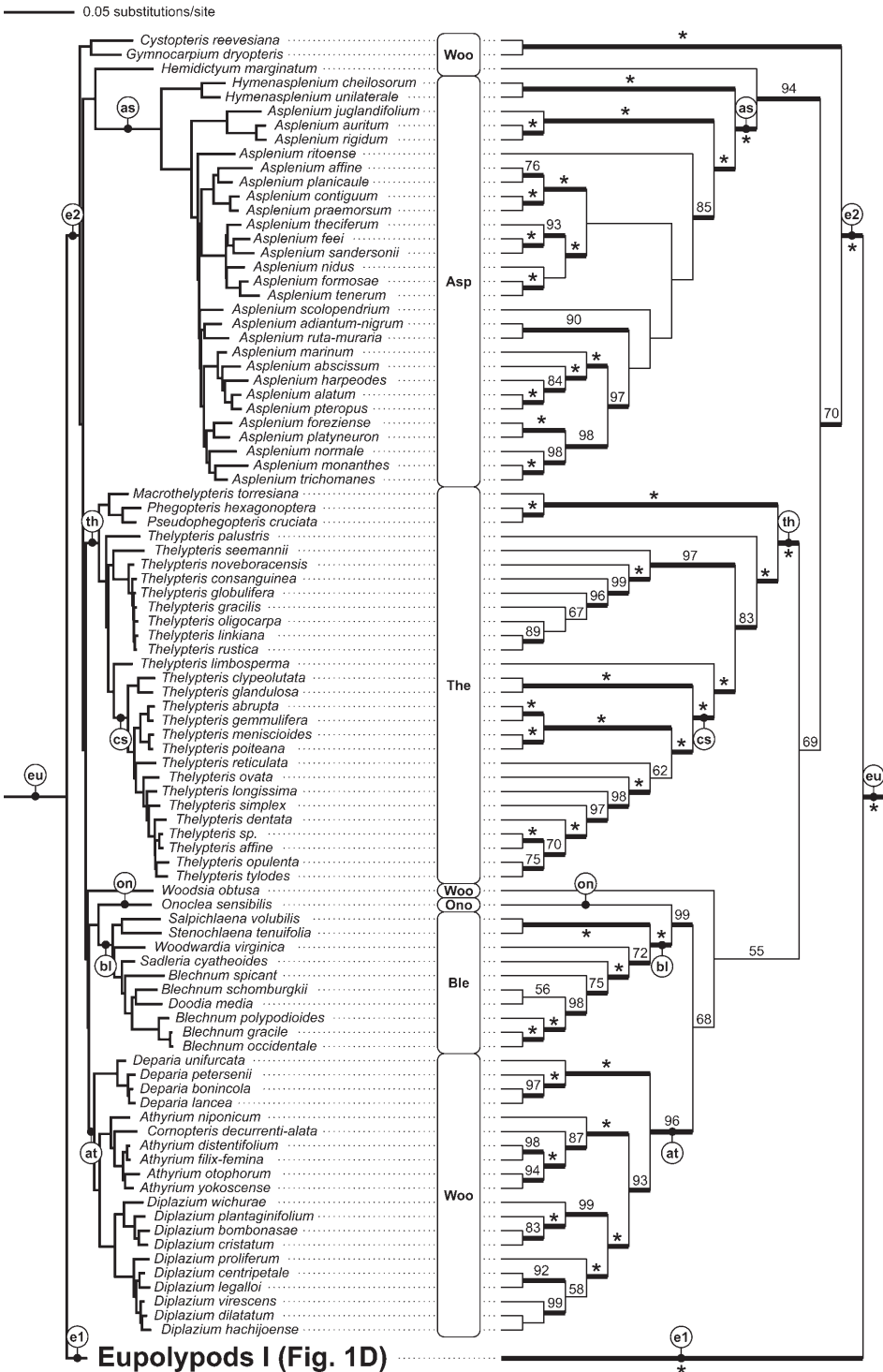


Fig. 1C. Continued from Fig. 1B. Major clades discussed in text are indicated in circles on trees: as, asplenioids; at, athyrioids; bl, blechnoids; cs, cyclosoroids; e1, eupolypods I; e2, eupolypods II; eu, eupolypods; on, onocleoids; th, thelypteroids. Families recognized in the most recent classification of extant ferns (Smith & al., 2006b) are indicated in boxes between trees: Asp, Aspleniaceae; Ble, Blechnaceae; Ono, Onocleaceae; The, Thelypteridaceae; Woo, Woodsiaceae. Phylogeny continues in Fig. 1D.

large clade of onocleoid (on), blechnoid (bl), and athyrioid (at) ferns (Fig. 1C). Smith & al. (2006b) tentatively placed all four of these genera in the Woodsiaceae (Woo, Fig. 1C). Now, however, it seems clear that this circumscription is paraphyletic, and the recognition of several additional families may well be warranted.

The athyrioid ferns (at, Fig. 1C), which account for most of the diversity in the Woodsiaceae, are indeed monophyletic (BS = 96%). The phylogeny of these ferns was the subject of two recent studies (Sano & al., 2000; Wang & al., 2003), and our results are in general accord with theirs. Our three-gene analysis does, however, find strong support ( $\geq 70\%$ ) for the fundamental splits within the clade (e.g., *Deparia* as sister to the remaining athyrioids) that were not well-supported in earlier single-gene analyses. The large genus *Athyrium* is not monophyletic (BS = 87%, Fig. 1C), but *Diplazium* as currently circumscribed may well be (but see Wang & al., 2003).

The asplenioid ferns (as, Fig. 1C) are also strongly supported as monophyletic in our analyses (BS = 100%), as they have been in earlier studies (Murakami & Schaal, 1994; Murakami & al., 1999; Gastony & Johnson, 2001; Pinter & al., 2002; Schneider & al., 2004b, 2005; Perrie & Brownsey, 2005). These earlier studies clearly demonstrated that nearly all genera previously segregated from *Asplenium* (e.g., *Camptosorus*, *Diellia*, and *Loxoscaphe*) nest well within this large genus. Thus, in the most recent classification (Smith & al., 2006b) only two genera were recognized in the Aspleniaceae (Asp)—*Hymenasplenium* being sister to *Asplenium* (Fig. 1C).

The thelypteroid ferns (th, Fig. 1C) compose a well-supported clade within eupolypods II (BS = 100%) and are recognized as a large family (Thelypteridaceae) with five genera by Smith & al. (2006b). In our study, the three smaller genera (*Macrothelypteris*, *Phegopteris*, and *Pseudophegopteris*) form a clade sister to the two larger genera (*Cyclosorus* and *Thelypteris*; note, however, that all species potentially assignable to *Cyclosorus* are presented here under *Thelypteris* to circumvent a variety of nomenclatural issues). The relationships we uncover within this larger clade are generally in agreement with those found in the only other study to examine thelypteroid phylogeny (Smith & Cranfill, 2002). In the earlier study, *Thelypteris* (sensu Smith, 1990) was not resolved as monophyletic; here, it is definitively paraphyletic to the cyclosoroids (BS = 100%, cs, Fig. 1C). Although our results do support the monophyly of several subgeneric groupings (e.g., *Amauropelta* and *Goniopteris*, not shown; Smith, 1990), we find strong support for the polyphyly of at least one of these groups—subgenus *Pronephrum* (*T. affine*, *T. simplex*, and *T. sp.* in Fig. 1C). Clearly, the thelypteroid clade is in need of additional phylogenetic study.

The onocleoid ferns (on, Fig. 1C), including *Onoclea* and three other small genera not sampled here (Gastony &

Ungerer, 1997; Smith & al., 2006b), are sister to a larger blechnoid clade (bl, Fig. 1C) that was the subject of three recent studies (Cranfill, 2001; Cranfill & Kato, 2003; Nakahira, 2000). Our results are in general accord with their more densely-sampled analyses: *Blechnum* is definitely not monophyletic (BS = 98%) and blechnoid taxonomy requires further attention.

#### Divergences within eupolypods I (Fig. 1D–E).

— Three genera not traditionally thought to be closely related to one another form a small, but poorly supported clade sister to the rest of eupolypods I (Fig. 1D). In earlier classifications (e.g., Kramer & al., 1990), *Didymochlaena* was considered to be associated with the dryopteroid ferns (dr, Fig. 1D); *Hypodematum* with the athyrioid ferns (at, Fig. 1C); and *Leucostegia* among the davallioid ferns (da, Fig. 1E). Previous studies found these genera to be rather isolated (Hasebe & al., 1995; Schneider & al., 2004c; Tsutsumi & Kato, 2006), but all three were never included in the same analysis as they are here. Our finding of good support (BS = 84%) for the monophyly of the remaining eupolypods I—excluding *Didymochlaena*, *Hypodematum*, and *Leucostegia*—is the first convincing evidence that these three genera should indeed be segregated from the Dryopteridaceae, where they were tentatively placed by Smith & al. (2006b), because they render it paraphyletic (Fig. 1D).

The dryopteroid ferns (dr) form a very large (about 1,700 species total) and well-supported clade (BS = 100%), with most “former lomariopsid” genera (fl) nested within it (Fig. 1D). Notably absent from the dryopteroid clade, however, is the genus *Lomariopsis* itself, which is resolved elsewhere in the eupolypods I clade (Fig. 1E). This suggests that the distinctive rhizome anatomy (with an elongated ventral meristele) characteristic of lomariopsid ferns has apparently evolved at least twice. While some large genera in the dryopteroid clade are the focus of extensive and ongoing phylogenetic studies (e.g., *Polystichum*, *Dryopteris*, and *Elaphoglossum*), other genera and the overall phylogeny of the group have received little or no attention (but see Li & Lu, 2006). Our analysis therefore provides considerable insight into the phylogeny of these ferns (despite relatively poor support for some early divergences).

The well-studied genera *Dryopteris* (Geiger & Ranker, 2005) and *Polystichum* (Little & Barrington, 2003; Li & al., 2004) compose a large well-supported clade together with *Phanerophlebia*, *Cyrtomium*, and *Arachniodes* (BS = 97%, Fig. 1D). The genus *Polystichopsis*—which is often synonymized under *Arachniodes* (e.g., Kramer & al., 1990)—is, however, not closely related to this clade. Rather, it is sister to a clade of “dimorphic climbers”—dryopteroid genera with creeping (to climbing) stems and dimorphic leaves (dc, Fig. 1D). *Stigmatopteris*, as well as *Ctenitis*, are both rather isolated within the dryopteroid



clade, 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 (fl, Fig. 1D), within which *Bolbitis* is resolved as polyphyletic. The relationships we resolve within the large genus *Elaphoglossum* are in general agreement with those from recent studies (Rouhan & al., 2004; Skog & al., 2004).

Within the eupolypods I, *Nephrolepis*, *Cyclopeltis*, and *Lomariopsis* also form a clade (Fig. 1E). Although this assemblage has not been resolved previously in its entirety (see Tsutsumi & Kato, 2006), and is in fact poorly-supported here, its monophyly is reinforced by a morphological synapomorphy—specifically the presence

of articulate pinnae. This clade is tentatively recognized as the Lomariopsidaceae in the most recent classification (Smith & al., 2006b). The oleandroid ferns, on the other hand, were thought to compose a natural group (Kramer, 1990) but are resolved here as definitively not monophyletic. We find strong support (BS = 75%) for *Arthropteris* and *Psammiosorus* as sister to the tectarioid ferns (te, Fig. 1E), and they are now included in the Tectariaceae (Tec, Fig. 1E; Smith & al., 2006b). *Oleandra* itself is sister to a large clade of davallioid (da) and polygrammoid (pg) ferns (BS = 96%, Fig. 1E), and is now considered to be the sole genus in Oleandraceae (Smith & al., 2006b).

The phylogeny of davallioid and polygrammoid ferns has been extremely well-studied in recent years (Schnei-

**Eupolypods I**

Phylogram (with branch lengths)

Cladogram (with branch support)

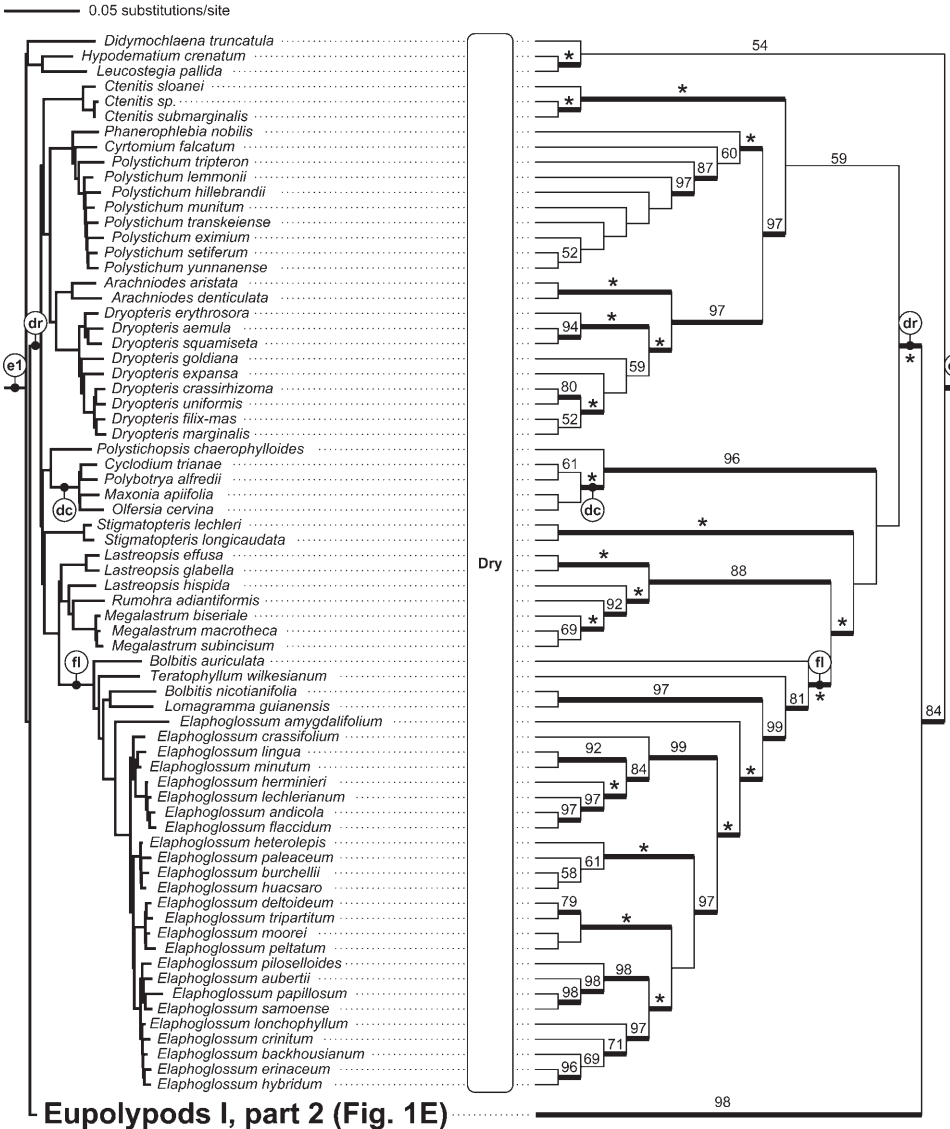


Fig. 1D. Continued from Fig. 1C. Major clades discussed in text are indicated in circles on trees: dc, dimorphic climbers; dr, dryopteroids; e1, eupolypods I; fl, former lomariopsids. Family recognized in the most recent classification of extant ferns (Smith & al., 2006b) is indicated in box between trees: Dry, Dryopteridaceae. Phylogeny continues in Fig. 1E.

der & al., 2002, 2004a, d, 2006a, b; Haufler & al., 2003; Ranker & al., 2003, 2004; Janssen & Schneider, 2005; Tsutsumi & Kato, 2005, 2006; Kreier & Schneider, 2006a, b), and the relationships we resolve within these clades are generally consistent with those resolved in earlier studies. As previously determined, the grammitid ferns (gr, Fig. 1E; Grammitidaceae sensu Parris, 1990) are nested firmly within the Polypodiaceae sensu Hennipman & al. (1990). Here we find strong support for the newly described genus *Serpocaulon* (Smith & al., 2006a) as sister to the grammitid clade (Fig. 1E).

## SUMMARY AND FUTURE PROSPECTS

Our three-gene analysis of 400 leptosporangiate species has resulted in by far the most comprehensive and well-supported assessment of fern phylogeny to date, providing an unparalleled framework within which to explore large-scale evolutionary patterns. However, with less than perfect levels of branch support and with more than 25% of fern genera and 95% of fern species still unaccounted for, it is clear that much work remains

### Eupolypods I, part 2

Phylogram (with branch lengths) ..... Fam ..... Cladogram (with branch support)

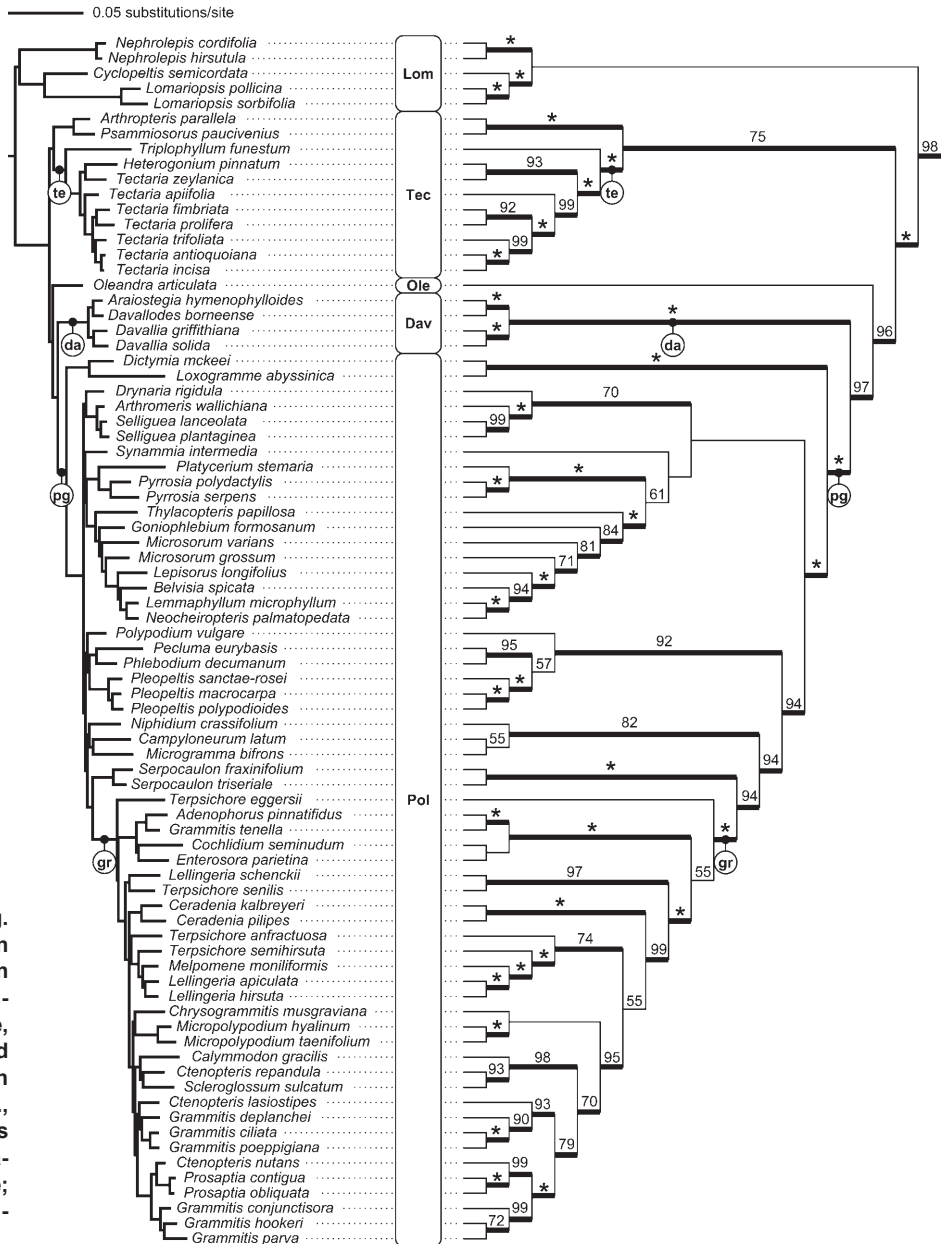


Fig. 1E. Continued from Fig. 1D. Major clades discussed in text are indicated in circles on trees: da, davallioids; gr, grammitids; pg, polygrammoids; te, tectarioids. Families recognized in the most recent classification of extant ferns (Smith & al., 2006b) are indicated in boxes between trees: Dav, Davalliaceae; Lom, Lomariopsidaceae; Ole, Oleandraceae; Pol, Polypodiaceae; Tec, Tectariaceae.

to be done. We have identified here several areas within the leptosporangiate fern phylogeny that are in need of further study. By continuing to include more taxa and additional data we will be able to move even closer to a full understanding of fern evolution and diversification.

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**Appendix 1. Taxonomic sampling for this study of leptosporangiate fern phylogeny.**

Species are arranged alphabetically under families recognized in the most recent classification of extant ferns (Smith & al., 2006b; Fig. 1). Fern DNA Database record numbers ([www.biology.duke.edu/pryerlab/ferndb](http://www.biology.duke.edu/pryerlab/ferndb); #NA = not available), voucher (collector, collection number, herbarium, locality) or publication information, and GenBank accession numbers are provided for sequences utilized (*rbcL*, *atpB*, and *atpA*, listed respectively).

**Anemiaceae:** *Anemia adiantifolia* (L.) Sw., #NA, Wikström & al., 2002, AJ303395, #2502, *Horn 507* (DUKE), Florida, U.S.A., EF463320, EF463583; *A. phyllitidis* (L.) Sw., #NA, Wikström & al., 2002, AJ303391, #3, Pryer & al., 2004, AY612687, *Lankester s.n.* (UC), Costa Rica, EF463584; *A. rotundifolia* Schrad., #3567, *Schuettelpelz 512* (GOET), in cultivation, EF463140, EF463321, EF463585; *A. tomentosa* (Savigny) Sw., #3568, *Schuettelpelz 513* (GOET), in cultivation, EF463141, EF463322, EF463586; **Aspleniaceae:** *Asplenium abscissum* Willd., #3553, *Jimenez 2503* (LPB), Bolivia, EF463142, EF463323, EF463587; *A. adiantum-nigrum* L., #3125, *Schuettelpelz 418* (DUKE), Arizona, U.S.A., EF463143, EF463324, EF463588; *A. affine* Sw., #3554, *Janssen 2719* (P), Reunion, EF463144, EF463325, EF463589; *A. alatum* Humb. & Bonpl. ex Willd., #2425, *Schuettelpelz 257* (DUKE), Ecuador, EF463145, EF463326, EF463590; *A. auritum* Sw., #3482, *Schneider s.n.* (GOET), in cultivation, EF463146, EF463327, EF463591; *A. contiguum* Kaulf., #3483, *Ranker 1876* (COLO), Hawaii, U.S.A., EF463147, EF463328, EF463592; *A. feei* Kunze ex Fée, #NA, Pinter & al., 2002, AF525267, #3478, *Lemieux 2272* (COLO), Costa Rica, EF463329, EF463593; *A. foreziense* Legrand ex Hérub., #3591, *Schuettelpelz 536* (GOET), in cultivation, EF463148, EF463330, EF463594; *A. formosae* H. Christ, #3484, *Ranker 2071* (COLO), Taiwan, EF463149, EF463331, EF463595; *A. harpeodes* Kunze, #3464, *Schneider s.n.* (GOET), in cultivation, EF463150, EF463332, EF463596; *A. juglandifolium* Lam., #3465, *Schneider s.n.* (GOET), in cultivation, EF463151, EF463333, EF463597; *A. marinum* L., #NA, Pinter & al., 2002, AF240647, #2952, *Christenhusz 3724* (TUR), Scotland, U.K., EF463334, EF463598; *A. monanthes* L., #NA, Schneider & al., 2004b, AY300125, #3552, *Lemieux 2324* (COLO), Costa Rica, EF463335, EF463599; *A. nidus* L., #NA, Pinter & al., 2002, AF525270, #11, *Fischer T-9* (UC), Madagascar, EF463336, EF463600; *A. normale* D. Don, #3466, *Ranker 2008* (COLO), Taiwan, EF463152, EF463337, EF463601; *A. planicaule* Lowe, #3467, *Ranker 2085* (COLO), Taiwan, EF463153, EF463338, EF463602; *A. platyneuron* (L.) Britton, Sterns & Poggenb., #NA, Pinter & al., 2002, AF525272, #3040, *Schuettelpelz 396* (DUKE), in cultivation, EF463339, EF463603; *A. praemorsum* Sw., #3578, *Schuettelpelz 523* (GOET), in cultivation, EF463154, EF463340, EF463604; *A. pteropus* Kaulf., #3468, *Ranker 1843* (COLO), Costa Rica, EF463155, EF463341, EF463605; *A. rigidum* Sw., #3469, *Lemieux 2277* (COLO), Costa Rica, EF463156, EF463342, EF463606; *A. ritoense* Hayata, #NA, Murakami & al., 1999, AB014692, #3479, *Ranker 2063* (COLO), Taiwan, EF463343, EF463607; *A. ruta-muraria* L., #NA, Pinter & al., 2002, AF525273, #2947, *Christenhusz 3869* (TUR), Scotland, U.K., EF463344, EF463608; *A. sandersonii* Hook., #NA, Pinter & al., 2002, AF525274, #3574, *Schuettelpelz 519* (GOET), in cultivation, EF463345, EF463609; *A. scolopendrium* L., #NA, Pinter & al., 2002, AF240645, #2945, *Christenhusz 3867* (TUR), Scotland, U.K., EF463346, EF463610; *A. tenerum* G. Forst., #NA, Schneider & al., 2004b, AY300145, #3480, *Ranker 1964* (COLO), Moorea, EF463347, EF463611; *A. theciferum* (Kunth) Mett., #NA, Gastony & Johnson, 2001, AF336099, #2426, *Schuettelpelz 258* (DUKE), Ecuador, EF463348, EF463612; *A. trichomanes* L., #3129, *Schuettelpelz 422* (DUKE), Arizona, U.S.A., EF463157, EF463349, EF463613; *Hymenasplenium cheilosorum* (Kunze ex Mett.) Tagawa, #NA, Murakami & al., 1999, AB014704, #3529, *Schäfer 55* (GOET), Yunnan, China, EF463350, EF463614; *H. unilaterale* (Lam.) Hayata, #3470, Schuettelpelz & al., 2007, EF452140, EF452020, EF452078; **Blechnaceae:** *Blechnum gracile* Kaulf., #2553, *Schuettelpelz 293* (DUKE), in cultivation, EF463158, EF463351, EF463615; *B. occidentale* L., #67, Wolf & al., 1994, U05910, Wolf, 1997, U93838, Schuettelpelz & al., 2007, EF452080; *B. polyodioides* Raddi, #2554, *Schuettelpelz 294* (DUKE), in cultivation, EF463159, EF463352, EF463616; *B. schomburgkii* (Klotzsch) C. Chr., #2410, *Schuettelpelz 242* (DUKE), Ecuador, EF463160, EF463353, EF463617; *B. spicant* (L.) Sm., #NA, Nakahira & Kato, unpublished, AB040571, #3212, *Christenhusz 3874* (TUR), Netherlands, EF463354, EF463618; *Doodia media* R. Br., #70, Wolf & al., 1994, U05922, #2555, *Schuettelpelz 295* (DUKE), in cultivation, EF463355, EF463619; *Sadleria cyatheoides* Kaulf., #3432, *Schuettelpelz 507* (DUKE), in cultivation, EF463161, EF463356, EF463620; *Salpichlaena volubilis* (Kaulf.) J. Sm., #3256, *Christenhusz 3949* (TUR), Guadeloupe, EF463162, EF463357, EF463621; *Stenochlaena tenuifolia* (Desv.) Moore, #3429, *Schuettelpelz 504* (DUKE), in cultivation, EF463163, EF463358, EF463622; *Woodwardia virginica* (L.) Sm., #NA, Cranfill & Kato, unpublished, AY137660, #2632, *Christenhusz 3810* (DUKE), North Carolina, U.S.A., EF463359, EF463623; **Cibotiaceae:** *Cibotium schiedei* Schltdl. & Cham., #2481, Korall & al., 2006b, AM177331, AM176593, *Morter 4* (E), in cultivation, EF463624; **Culcitaceae:** *Culcita conifolia* (Hook.) Maxon, #2363, Korall & al., 2006b, AM177333, AM176595, *Conant 4405* (LSC), Costa Rica, EF463625; **Cyatheaceae:** *Alsophila bryophila* R. Tryon, #2304, Korall & al., 2006b, AM177320, AM176581, *Conant 4322* (LSC), Puerto Rico, EF463626; *A. capensis* (L. f.) J. Sm., #2326, Korall & al., 2006b, AM177321, AM176582, *Shirley 14* (LSC), Africa, EF463627; *A. colensoi* Hook. f., #2329, Korall & al., 2006b, AM177322, AM176583, *Shirley 1* (LSC), New Caledonia, EF463628; *A. cuspidata* (Kunze) D.S. Conant, #2334, Korall & al., 2006b, AM177323, AM176584, *Conant 4427* (LSC), Costa Rica, EF463629; *A. dregei* (Kunze) R.M. Tryon, #2325, Korall & al., 2007, AM410194, *Shirley 13* (LSC), Africa, EF463360, EF463630; *A. foersteri* (Rosenst.) R.M. Tryon, #2337, Korall & al., 2006b, AM177324, AM176585, *Conant 4646* (LSC), Papua New Guinea, EF463631; *A. hooglandii* (Holt.) R.M. Tryon, #2315, Korall & al., 2006b, AM177325, AM176586, *Conant 4650* (LSC), Papua New Guinea, EF463632; *A. ramispina* Hook., #2335, Korall & al., 2006b, AM177326, AM176587, *Conant 4706* (LSC), Borneo, EF463633; *A. salvinii* Hook., #2306, Korall & al., 2007, AM410184, *Conant 4365* (LSC), Honduras, EF463361, EF463634; *A. stelligera* (Holt.) R.M. Tryon, #2338, Korall & al., 2007, AM410198, *Pintaud 411* (LSC), New Caledonia, EF463362, EF463635; *Cyathea alata* (E. Fourn.) Copel., #2328, *Pintaud 414* (LSC), New Caledonia, EF463164, EF463363, EF463636; *C. horrida* (L.) Sm., #2331, Korall & al., 2007, AM410196, *Conant 4343* (LSC), Puerto Rico, EF463364, EF463637; *C. multiflora* Sm., #2333, Korall & al., 2007, AM410197, *Conant 4425* (LSC), Costa Rica, EF463365, EF463638; *C. parvula* (Jenm.) Proctor, #2330, Korall & al., 2006b, AM177338, AM176600, *Conant 4332* (LSC), Puerto Rico, EF463639; *C. poeppigii* (Hook.) Domin, #80, Pryer & al., 2001a, AF313585, AF313553, #2367, *Conant 4410* (LSC), Costa Rica, EF463640; *Hymenophyllopsis dejecta* (Baker) Goebel, #397, Wolf & al., 1999, AF101301, Pryer & al., 2004, AY612698, *Milleron s.n.* (UC), Venezuela, EF463641; *Sphaeropteris capitata* (Copel.) R.M. Tryon, #2321, Korall & al., 2007, AM410192, *Conant 4710* (LSC), Borneo, EF463366,

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## Appendix 1. Continued.

EF463642; *S. celebica* (Blume) R.M. Tryon, #2327, Korall & al., 2007, AM410195, *Shirley 02* (LSC), Australia, EF463367, EF463643; *S. horrida* (Liebm.) R.M. Tryon, #2340, Korall & al., 2007, AM410200, *Conant 4363* (LSC), Honduras, EF463368, EF463644; *S. medullaris* (Forst. f.) Bernh., #2323, Korall & al., 2006b, AM177350, AM176617, *Shirley 07* (LSC), New Zealand, EF463645; *S. megalosora* (Copel.) R.M. Tryon, #2319, Korall & al., 2007, AM410190, *Conant 4702* (LSC), Borneo, EF463369, EF463646; *S. robusta* (Watts) R.M. Tryon, #2316, Korall & al., 2007, AM410187, *Conant 4663* (LSC), Lord Howe Island, Australia, EF463370, EF463647; **Davalliaceae:** *Araiostegia hymenophylloides* (Blume) Copel., #NA, Tsutsumi & Kato, 2005, AB212689, AB212689, #3739, *Huiet s.n.* (UC), in cultivation, EF463648; *Davallia griffithiana* Hook., #3431, *Schuettpelz 506* (DUKE), in cultivation, EF463165, EF463371, EF463649; *D. solida* (G. Forst.) Sw., #NA, Tsutsumi & Kato, 2005, AB212712, #2560, Schuettpelz & al., 2007, EF452029, EF452089; *Davallodes borneense* (Hook.) Copel., #NA, Tsutsumi & Kato, 2005, AB212694, AB212694, #3615, *Schuettpelz 560* (GOET), in cultivation, EF463650; **Dennstaedtiaceae:** *Blotiella pubescens* (Willd. ex Kaulf.) R.M. Tryon, #88, Wolf & al., 1994, U05911, *Strasberg s.n.* (UTC), Reunion, EF463372, EF463651; *Dennstaedtia dissecta* (Sw.) T. Moore, #2465, *Schuettpelz 9* (DUKE), Costa Rica, EF463166, EF463373, EF463652; *D. punctilobula* (Michx.) T. Moore, #99, Wolf & al., 1994, U05918, Wolf, 1997, U93836, Schuettpelz & al., 2007, EF452090; *Histiopteris incisa* (Thunb.) J. Sm., #102, Wolf & al., 1994, U05926, *Smith s.n.* (UC), in cultivation, EF463374, EF463653; *Hypolepis tenuifolia* (G. Forst.) Bernh., #2547, *Schuettpelz 286* (DUKE), in cultivation, EF463167, EF463375, EF463654; *Leptolepia novae-zelandiae* (Col.) Mett. ex Diels, #3061, *Parris 12400* (DUKE), New Zealand, EF463168, EF463376, EF463655; *Microlepia platyphylla* (D. Don) J. Sm., #114, Wolf, 1995, U18642, Wolf, 1997, U93832, Schuettpelz & al., 2007, EF452101; *M. spelunca* (L.) T. Moore, #2550, *Schuettpelz 289* (DUKE), in cultivation, EF463169, EF463377, EF463656; *Monachosorum henryi* H. Christ, #478, Wolf & al., 1994, U05932, Pryer & al., 2004, AY612706, Korall & al., 2006b, AM176469; *Paesia scaberula* (A. Rich) Kuhn, #119, Wolf & al., 1994, U05937, Wolf 387 (UTC), in cultivation, EF463378, EF463657; *Pteridium esculentum* (G. Forst.) Nakai, #125, Wolf & al., 1994, U05940, #NA, Wolf, 1997, U93834, #125, Schuettpelz & al., 2007, EF452115; **Dicksoniaceae:** *Calochlaena villosa* (C. Chr.) M.D. Turner & R.A. White, #2254, Korall & al., 2006b, AM177327, AM176588, *Woodhaus s.n.* (AAU), in cultivation, EF463658; *Dicksonia antarctica* Labill., #134, Wolf & al., 1994, U05919, Wolf, 1997, U93829, *Wolf 276* (UTC), in cultivation, EF463659; *Lophosoria quadripinnata* (J.F. Gmel.) C. Chr., #424, Wolf & al., 1999, AF101303, Pryer & al., 2004, AY612701, Grantham 006-92 (UC), Chile, EF463660; **Dipteridaceae:** *Cheiropleuria integrifolia* (D.C. Eaton ex Hook.) M. Kato, Y. Yatabe, Sahashi & N. Murak., #NA, Kato & al., 2001, AB042569, #75, Pryer & al., 2004, AY612692, *Yokoyama 27619* (TI), Japan, EF463661; *Dipteris conjugata* Reinw., #141, Hasebe & al., 1994, U05620, #140, Pryer & al., 2004, AY612696, *Game 98/106* (UC), Fiji, EF463662; **Dryopteridaceae:** *Arachniodes aristata* (G. Forst.) Tindale, #NA, Geiger & Ranker, 2005, AY268851, #3613, *Schuettpelz 558* (GOET), in cultivation, EF463379, EF463663; *A. denticulata* (Sw.) Ching, #NA, Little & Barrington, 2003, AF537223, #3502, *Barrington 2130* (VT), Costa Rica, EF463380, EF463664; *Bolbitis auriculata* (Lam.) Alston, #3504, *Rakotondrainibe 6611* (P), Comoros, EF463170, EF463381, EF463665; *B. nicotianifolia* (Sw.) Alston, #3327, *Christenhusz 4062* (TUR), Guadeloupe, EF463171, EF463382, EF463666; *Ctenitis sloanei* (Poep. ex Spreng.) C.V. Morton, #3607, *Schuettpelz 552* (GOET), in cultivation, EF463172, EF463383, EF463667; *C. sp.*, #3577, *Schuettpelz 522* (GOET), in cultivation, EF463174, EF463385, EF463669; *C. submarginalis* (Langsd. & Fisch.) Ching, #2464, *Schuettpelz 1* (DUKE), Costa Rica, EF463173, EF463384, EF463668; *Cyclodium trianae* (Mett.) A.R. Sm., #3770, *Moran 7466* (NY), Ecuador, EF463175, EF463386, EF463670; *Cyrtomium falcatum* (L. f.) C. Presl, #2937, *Little 342* (VT), in cultivation, EF463176, EF463387, EF463671; *Didymochlaena truncatula* (Sw.) J. Sm., #NA, Smith & Cranfill, 2002, AF425105, #2435, Schuettpelz & al., 2007, EF452030, EF452091; *Dryopteris aemula* (Aiton) Kuntze, #NA, Geiger & Ranker, 2005, AY268881, #2944, Schuettpelz & al., 2007, EF452033, EF452094; *D. crassirhizoma* Nakai, #3036, *Schuettpelz 392* (DUKE), in cultivation, EF463177, EF463388, EF463672; *D. erythrosora* (D.C. Eaton) Kuntze, #3593, *Schuettpelz 538* (GOET), in cultivation, EF463178, EF463389, EF463673; *D. expansa* (C. Presl) Fraser-Jenk. & Jermy, #3496, *Christenhusz 4263* (TUR), Finland, EF463179, EF463390, EF463674; *D. filix-mas* (L.) Schott, #3121, *Schuettpelz 414* (DUKE), Arizona, U.S.A., EF463180, EF463391, EF463675; *D. goldiana* (Hook. ex Goldie) A. Gray, #NA, Little & Barrington, 2003, AF537228, #2938, *Barrington 2123* (VT), Vermont, U.S.A., EF463392, EF463676; *D. marginalis* (L.) A. Gray, #2979, *Schuettpelz 334* (DUKE), in cultivation, EF463181, EF463393, EF463677; *D. squamiseta* (Hook.) Kuntze, #3557, *Janssen 2714* (P), Reunion, EF463182, EF463394, EF463678; *D. uniformis* (Makino) Makino, #3592, *Schuettpelz 537* (GOET), in cultivation, EF463183, EF463395, EF463679; *Elaphoglossum amygdalifolium* (Mett. ex Kuhn) H. Christ, #2673, *Moran 6952* (NY), Ecuador, EF463184, EF463396, EF463680; *E. andicola* (Fée) T. Moore, #2674, *Bach 1697* (GOET), Bolivia, EF463185, EF463397, EF463681; *E. aubertii* (Desv.) T. Moore, #2689, *Hemp 8* (E), Tanzania, EF463186, EF463398, EF463682; *E. backhousianum* T. Moore, #2690, *Moran s.n.* (NY), in cultivation, EF463187, EF463399, EF463683; *E. burchellii* (Baker) C. Chr., #NA, Skog & al., 2004, AY818683, #3461, *Moran s.n.* (NY), in cultivation, EF463400, EF463684; *E. crassifolium* (Gaudich.) W.R. Anderson & Crosby, #2676, *Mickel 9703* (NY), Hawaii, U.S.A., EF463188, EF463401, EF463685; *E. crinitum* (L.) H. Christ, #2685, *Trusty 70* (CR), Costa Rica, EF463189, EF463402, EF463686; *E. deltoideum* (Sodiolo) H. Christ, #2694, *Moran 6867* (NY), Ecuador, EF463190, EF463403, EF463687; *E. erinaceum* (Fée) T. Moore, #2686, *Blanco 2231* (USJ), Costa Rica, EF463191, EF463404, EF463688; *E. flaccidum* (Fée) T. Moore, #2374, *Schuettpelz 206* (DUKE), Ecuador, EF463192, EF463405, EF463689; *E. herminieri* (Bory ex Fée) T. Moore, #2677, *Moran s.n.* (NY), in cultivation, EF463193, EF463406, EF463690; *E. heterolepis* (Fée) T. Moore, #2683, *Ranker 1414* (COLO), Reunion, EF463194, EF463407, EF463691; *E. huacsaro* (Ruiz) H. Christ, #2680, *Nee 52309* (NY), Dominican Republic, EF463195, EF463408, EF463692; *E. hybridum* (Bory) Brack., #2687, *Motley 2912* (NY), Reunion, EF463196, EF463409, EF463693; *E. lechlerianum* (Mett.) T. Moore, #2678, *Bach 1399* (GOET), Bolivia, EF463197, EF463410, EF463694; *E. lingua* (C. Presl) Brack., #NA, Skog & al., 2004, AY818697, #3459, *Moran 6380* (CR), Costa Rica, EF463411, EF463695; *E. lonchophyllum* (Fée) T. Moore, #3456, Skog & al., 2004, AY818698, *Hammer 9* (NY), Veracruz, Mexico, EF463412, EF463696; *E. minutum* (Pohl ex Fée) T. Moore, #NA, Skog & al., 2004, AY818699, #3457, *Moran 6334* (NY), Costa Rica, EF463413, EF463697; *E. moorei* (E. Britton) H. Christ, #2696, *Bach 1584* (GOET), Bolivia, EF463198, EF463414, EF463698; *E. paleaceum* (Hook. & Grev.) Sledge, #2681, *Moran s.n.* (NY), in cultivation, EF463199, EF463415, EF463699; *E. papillosum* (Baker) H. Christ, #3462, *Smith 2873* (NY), unknown, EF463200, EF463416, EF463700; *E. peltatum* (Sw.) Urb., #2697, *Moran*



## Appendix 1. Continued.

*s.n.* (NY), in cultivation, EF463201, EF463417, EF463701; *E. piloselloides* (C. Presl) T. Moore, #2691, *Labiak 2827* (NY), Bolivia, EF463202, EF463418, EF463702; *E. samoense* Brack., #2692, *Ranker 1907* (COLO), Tahiti, French Polynesia, EF463203, EF463419, EF463703; *E. tripartitum* (Hook. ex Grev.) Mickel, #2698, *Moran 6783* (NY), Ecuador, EF463204, EF463420, EF463704; *Hypodematum crenatum* (Forssk.) Kuhn, #3511, *Schneider s.n.* (GOET), in cultivation, EF463205, EF463421, EF463705; *Lastreopsis effusa* (Sw.) Tindale, #2939, Little & Barrington, 2003, AF537230, *Howlett s.n.* (VT), Costa Rica, EF463422, EF463706; *L. glabella* (A. Cunn. in Hook.) Tindale, #3635, *Schuettpeitz 580* (GOET), in cultivation, EF463206, EF463423, EF463707; *L. hispida* (Sw.) Tindale, #3512, *Schneider s.n.* (GOET), in cultivation, EF463207, EF463424, EF463708; *Leucostegia pallida* (Mett.) Copel., #NA, Tsutsumi & Kato, 2006, AB232389, #3652, *Schuettpeitz 605* (B), in cultivation, EF463425, EF463709; *Lomagramma guianensis* (Aubl.) Ching, #3416, *Christenhusz 4228* (TUR), Puerto Rico, EF463208, EF463426, EF463710; *Maxonia apiifolia* (Sw.) C. Chr., #3059, *Christenhusz 3390* (IJ), Jamaica, EF463209, EF463427, EF463711; *Megalastrum biseriale* (Baker) A.R. Sm. & R.C. Moran, #3758, *Moran 7545* (NY), Ecuador, EF463210, EF463428, EF463712; *M. macrotheca* (Fée) A.R. Smith & R.C. Moran, #3391, *Christenhusz 4181* (TUR), Guadeloupe, EF463211, EF463429, EF463713; *M. subincisum* (Willd.) A.R. Sm. & R.C. Moran, #3757, *Moran 7608* (NY), Ecuador, EF463212, EF463430, EF463714; *Olferisia cervina* (L.) Kunze, #3342, *Christenhusz 4082* (TUR), Guadeloupe, EF463213, EF463431, EF463715; *Phanerophlebia nobilis* (Schldl. & Cham.) C. Presl, #2940, *Yatskievych 85-211* (IND), Mexico, Mexico, EF463214, EF463432, EF463716; *Polybotrya alfredii* Brade, #3762, *Moran 7612* (NY), Ecuador, EF463215, EF463433, EF463717; *Polystichopsis chaerophylloides* (Poir.) C.V. Morton, #3413, *Christenhusz 4223* (TUR), Puerto Rico, EF463216, EF463434, EF463718; *Polystichum eximium* (Mett. ex Kuhn) C. Chr., #NA, Li & al., 2004, AY545493, #2928, *Barrington 2085* (VT), Yunnan, China, EF463435, EF463719; *P. hillebrandii* Carruth., #2929, *Driscoll 310* (VT), Hawaii, U.S.A., EF463217, EF463436, EF463720; *P. lemmonii* Underw., #2931, *Zika 10741* (VT), Washington, U.S.A., EF463218, EF463437, EF463721; *P. munitum* (Kaulf.) C. Presl, #NA, Little & Barrington, 2003, AF537261, #2930, *Zika 18930* (VT), Washington, U.S.A., EF463438, EF463722; *P. setiferum* (Forssk.) Moore ex Woytn., #NA, Little & Barrington, 2003, AF537254, #2932, *Mickel s.n.* (VT), in cultivation, EF463439, EF463723; *P. transkeiense* N. Jacobsen, #NA, Little & Barrington, 2003, AF537257, #2934, *Roux 2493* (VT), Africa, EF463440, EF463724; *P. tripterum* (Kunze) C. Presl, #2935, *Kato s.n.* (VT), in cultivation, EF463219, EF463441, EF463725; *P. yunnanense* H. Christ, #2936, *Barrington 2087* (VT), Yunnan, China, EF463220, EF463442, EF463726; *Rumohra adiantiformis* (G. Forst.) Ching, #157, Wolf & al., 1994, U05942, #2559, *Schuettpeitz 299* (DUKE), in cultivation, EF463443, EF463727; *Stigmatopteris lechleri* (Mett.) C. Chr., #3755, *Moran 3026* (CR), Costa Rica, EF463221, EF463444, EF463728; *S. longicaudata* (Liebm.) C. Chr., #2941, *Barrington 2099A* (VT), Costa Rica, EF463222, EF463445, EF463729; *Teratophyllum wilkesianum* (Brack.) Holttum, #3723, *Murdock 131* (UC), Moorea, French Polynesia, EF463223, EF463446, EF463730; **Equisetaceae:** *Equisetum telmateia* Ehrh., #768, Pryer & al., 2001a, AF313580, AF313542, *Smith 2575* (UC), California, U.S.A., EF463731; *E. × ferrissii* Clute, #760, Pryer & al., 2001a, AF313579, AF313541, *Hammond s.n.* (UC), California, U.S.A., EF463732; **Gleicheniaceae:** *Dicranopteris linearis* (Burm. f.) Underw., #167, Wolf, 1995, U18626, #958, Pryer & al., 2004, AY612694, #171, *Lorence 7764* (PTBG), Hawaii, U.S.A., EF463733; *Diplopterygium bancroftii* (Hook.) A.R. Sm., #172, *Smith 2569* (UC), Veracruz, Mexico, EF463224, Pryer & al., 2004, AY612695, *Smith 2569* (UC), Veracruz, Mexico, EF463734; *Gleichenella pectinata* (Willd.) Ching, #3425, *Christenhusz 4240* (TUR), Puerto Rico, EF463225, #174, Pryer & al., 2004, AY612697, #3425, *Christenhusz 4240* (TUR), Puerto Rico, EF463735; *Gleichenia dicarpa* R. Br., #883, Pryer & al., 2001a, AF313584, AF313550, *Cranfill 227* (UC), New Zealand, EF463736; *Sticherus bifidus* (Willd.) Ching, #176, *Smith 2565* (UC), Veracruz, Mexico, EF463226, EF463447, EF463737; *S. palmatus* (W. Schaffn. ex E. Fourn.) Copel., #177, Pryer & al., 2004, AY612684, AY612711, *Smith 2568* (UC), Veracruz, Mexico, EF463738; *Stromatopteris moniliformis* Mett., #915, Pryer & al., 2004, AY612685, *van der Werff 16076* (UC), New Caledonia, EF463448, EF463739; **Hymenophyllaceae:** *Abrodictyum elongatum* (A. Cunn.) Ebihara & K. Iwats., #936, Dubuisson & al., 2003, AY175802, *Smith 2604* (UC), New Zealand, EF463449, EF463740; *Cephalomanes javanicum* (Blume) C. Presl, #900, Dubuisson, 1997, Y09195, *Edwards s.n.* (MPU), Brunei, EF463450, EF463741; *Crepidomanes bipunctatum* (Poir.) Copel., #2646, *Hennequin 2002-9* (P), Reunion, EF463227, EF463451, EF463742; *C. minutum* (Blume) K. Iwats., #374, Hasebe & al., 1994, U05625, #2741, *Ebihara 001015-03* (T5), Japan, EF463452, EF463743; *C. thysanostomum* (Makino) Ebihara & K. Iwats., #389, Hasebe & al., 1994, U05608, *Hasebe 26549* (TI), Japan, EF463453, EF463744; *Didymoglossum ekmanii* (Wess. Boer) Ebihara & Dubuisson, #898, Dubuisson, 1997, Y09192, *Hallé s.n.* (MPU), Colombia, EF463454, EF463745; *D. krausii* (Hook. & Grev.) C. Presl, #2388, *Schuettpeitz 220* (DUKE), Ecuador, EF463228, EF463455, EF463746; *D. membranaceum* (L.) Vareschi, #901, Dubuisson, 1997, Y09197, #2652, *Dubuisson HG 2004-41* (P), Guadeloupe, EF463456, EF463747; *Hymenophyllum apiculatum* Mett. ex Kuhn, #864, Pryer & al., 2001b, AF275642, *Dubuisson HV1997-23* (F), Venezuela, EF463457, EF463748; *H. armstrongii* (Baker) Kirk, #939, Hennequin & al., 2003, AY095109, *Smith 2610* (UC), New Zealand, EF463458, EF463749; *H. baileyman* Domin, #851, Pryer & al., 2001b, AF275643, *Streimann s.n.* (UC), Queensland, Australia, EF463459, EF463750; *H. cruentum* Cav., #NA, Hennequin & al., 2003, AY095107, #1049, *Kelch 00.123B* (UC), Chile, EF463460, EF463751; *H. digitatum* (Sw.) Fosberg, #820, Pryer & al., 2001b, AF275651, *Game 86/08* (UC), Cook Islands, EF463461, EF463752; *H. dilatatum* (G. Forst.) Sw., #993, Hennequin & al., 2003, AY095111, *Brownsey s.n.* (DUKE), New Zealand, EF463462, EF463753; *H. fucooides* (Sw.) Sw., #346, Hasebe & al., 1995, U20933, #345, *Dubuisson HV1997-9* (F), Venezuela, EF463463, EF463754; *H. hirsutum* (L.) Sw., #853, Pryer & al., 2001b, AF275645, Pryer & al., 2001a, AF313538, *Kessler 9756* (UC), Bolivia, EF463755; *H. hygrometricum* (Poir.) Desv., #966, Hennequin & al., 2003, AY095113, *Dubuisson HR 1999-13* (DUKE), Reunion, EF463464, EF463756; *H. inaequale* (Poir.) Desv., #967, Hennequin & al., 2003, AY095112, #2953, *Hennequin 2002-12* (P), Reunion, EF463465, EF463757; *H. nephrophyllum* (G. Forst.) Ebihara & K. Iwats., #335, Hasebe & al., 1995, U30833, #935, *Smith 2606* (UC), New Zealand, EF463466, EF463758; *H. polyanthos* (Sw.) Sw., #854, Pryer & al., 2001b, AF275647, *Kessler 9866* (UC), Bolivia, EF463467, EF463759; *H. sibthorpioides* Mett., #968, Hennequin & al., 2003, AY095117, *Dubuisson HR 1999-1* (F), Reunion, EF463468, EF463760; *H. tunbigenense* (L.) Sm., #869, Dubuisson, 1997, Y09203, #2903, *Katzer 3* (P), Scotland, U.K., EF463469, EF463761; *Polyphlebium borbonicum* (Bosch) Ebihara & Dubuisson, #2071, Dubuisson & al., 2003, AY175782, *Dubuisson HR 1999-25* (P), Reunion, EF463470, EF463762; *P. endlicherianum* (C. Presl) Ebihara & K. Iwats., #948, *Smith 2600* (UC), New Zealand, EF463229, EF463471, EF463763; *Trichomanes ankersii* C. Parker ex

## Appendix 1. Continued.

Hook. & Grev., #859, Dubuisson & al., 2003, AY175800, *Hallé s.n.* (MPU), Colombia, EF463472, EF463764; *T. crispum* L., #862, Dubuisson & al., 2003, AY175789, *Dubuisson HV1997-22* (DUKE), Venezuela, EF463473, EF463765; *T. pinnatum* Hedw., #904, Dubuisson, 1997, Y09200, #1293, *Kessler 10872* (UC), Bolivia, EF463474, EF463766; *Vandenboschia radicans* (Sw.) Copel., #856, Pryer & al., 2001b, AF275650, #385, *Horich s.n.* (UC), Costa Rica, EF463475, EF463767; **Lindsaeaaceae:** *Cystodium sorbifolium* (Sm.) J. Sm., #2498, Korall & al., 2006a, AM184111, AM184112, *Christensen 1529* (S), Sarawak, Malaysia, EF463768; *Lindsaea blotiana* K.U. Kramer, #3508, *Rakotondrainibe 6350* (P), Madagascar, EF463230, EF463476, EF463769; *L. madagascariensis* Baker, #3507, *Rakotondrainibe 6349* (P), Madagascar, EF463231, EF463477, EF463770; *L. quadrangularis* Raddi, #3304, *Christenhusz 4018* (TUR), Guadeloupe, EF463232, EF463478, EF463771; *Lonchitis hirsuta* L., #112, Wolf & al., 1994, U05929, #414, Pryer & al., 2004, AY612700, *Axelrod 9601* (UTC), Puerto Rico, EF463772; *Odontosoria aculeata* (L.) J. Sm., #3427, *Christenhusz 4242* (TUR), Puerto Rico, EF463233, EF463479, EF463773; *Sphenomeris chinensis* (L.) Maxon, #411, Wolf & al., 1994, U05934, #408, Pryer & al., 2004, AY612710, #416, *Moore 20263* (DUKE), Taiwan, EF463774; **Lomariopsidaceae:** *Cyclopeltis semicordata* (Sw.) J. Sm., #3501, *Barrington 2129* (VT), Costa Rica, EF463234, EF463480, EF463775; *Lomariopsis pollicina* (Willemet) Mett. ex Kuhn, #3505, *Rakotondrainibe 6707* (P), Grande Comore, EF463235, EF463481, EF463776; *L. sorbifolia* (L.) Fée, #3333, *Christenhusz 4070* (TUR), Guadeloupe, EF463236, EF463482, EF463777; *Nephrolepis cordifolia* (L.) C. Presl, #479, Wolf & al., 1994, U05933, Schuettpeitz & al., 2007, EF452041, EF452103; *N. hirsutula* (G. Forst.) C. Presl, #3071, *Christenhusz 3580* (TUR), Puerto Rico, EF463237, EF463483, EF463778; **Loxomataceae:** *Loxoma cunninghamii* R. Br., #835, Pryer & al., 2004, AY612679, AY612702, *Cranfill s.n.* (UC), New Zealand, EF463779; *Loxosomopsis pearcei* (Baker) Maxon, #729, Pryer & al., 2004, AY612680, AY612703, *Sánchez Baracaldo 322* (UC), Ecuador, EF463780; **Lygodiaceae:** *Lygodium japonicum* (Thunb.) Sw., #440, Manhart, 1994, L13479, #441, Pryer & al., 2001a, AF313549, #2545, *Metzgar s.n.* (DUKE), in cultivation, EF463781; *L. reticulatum* Schkuhr, #3430, *Schuettpeitz 505* (DUKE), in cultivation, EF463238, EF463484, EF463782; **Marattiaceae:** *Angiopteris evecta* (G. Forst.) Hoffm., #2569, *Christenhusz 2992* (IJ), Jamaica, EF463239, EF463485, EF463783; *Danaea elliptica* Sm., #451, Pryer & al., 2001a, AF313578, AF313540, *Sharpe s.n.* (UC), Puerto Rico, EF463784; *Marattia alata* Sw., #2570, *Christenhusz 3266* (IJ), Jamaica, EF463240, EF463486, EF463785; **Marsileaceae:** *Marsilea drummondii* A. Braun, #463, *Hoshizaki 577* (UC), in cultivation, EF463241, Pryer & al., 2001a, AF313551, #2041, *Pryer s.n.* (no voucher), in cultivation, EF463786; *M. mutica* Mett., #2046, Korall & al., 2006b, AM177357, AM176623, *Nagalingum 25* (DUKE), in cultivation, EF463787; *Pilularia globulifera* L., #472, Pryer & al., 2004, AY612681, AY612707, #2048, *Schneider s.n.* (GOET), Germany, EF463788; **Matoniaceae:** *Matonia pectinata* R. Br., #NA, Kato & Setoguchi, 1998, AF012267, #475, Pryer & al., 2004, AY612704, *Hasebe 27620* (TI), Malaysia, EF463789; *Phanerogon sarmentosus* (Baker) Copel., #866, Pryer & al., 2001a, AF313583, AF313548, *Kato s.n.* (TI), Sarawak, Malaysia, EF463790; **Metaxyaceae:** *Metaxya rostrata* (Kunth.) C. Presl, #476, Smith & al., 2001, AF317699, Pryer & al., 2004, AY612705, #2305, *Conant 4355* (LSC), Honduras, EF463791; **Oleandraceae:** *Oleandra articulata* (Sw.) C. Presl, #3281, *Christenhusz 3980* (TUR), Guadeloupe, EF463242, EF463487, EF463792; **Onocleaceae:** *Onoclea sensibilis* L., #NA, Gastony & Ungerer, 1997, U62034, #2998, *Schuettpeitz 353* (DUKE), in cultivation, EF463488, EF463793; **Osmundaceae:** *Leptopteris wilkesiana* (Brack.) H. Christ, #492, Pryer & al., 2004, AY612678, AY612699, #912, *van der Werff 16025* (UC), New Caledonia, EF463794; *Osmunda cinnamomea* L., #NA, Yatabe & al., 1999, AB024949, #496, Pryer & al., 2001a, AF313539, #2596, *Christenhusz 3380* (IJ), Jamaica, EF463795; *Todea barbara* (L.) Moore, #NA, Yatabe & al., 1999, AB024959, #499, Pryer & al., 2004, AY612714, *Smith 2895* (UC), in cultivation, EF463796; **Plagiogyriaceae:** *Plagiogyria japonica* Nakai, #501, Hasebe & al., 1994, U05643, Pryer & al., 2001a, AF313547, *Hasebe 27614* (TI), Japan, EF463797; **Polypodiaceae:** *Adenophorus pinnatifidus* Gaudich., #187, Ranker & al., 2003, AF468201, AF469777, *Ranker 1559* (COLO), Hawaii, U.S.A., EF463798; *Arthromeris wallichiana* (Spreng.) Ching, #3541, *Schneider s.n.* (E), in cultivation, EF463243, EF463489, EF463799; *Belvisia spicata* (L. f.) Mirb., #3537, *Ranker 1915* (COLO), Tahiti, French Polynesia, EF463244, EF463490, EF463800; *Calymmodon gracilis* (Fée) Copel., #190, Ranker & al., 2004, AY362341, AY459451, *Chiou 97-09-12-01* (TAIF), Taiwan, EF463801; *Campyloneurum latum* T. Moore, #3257, *Christenhusz 3950* (TUR), Guadeloupe, EF463245, EF463491, EF463802; *Ceradenia kalbreyeri* (Baker) L.E. Bishop, #2662, Ranker & al., 2004, AY460621, AY459455, *Rojas 3223* (no voucher), Costa Rica, EF463803; *C. pilipes* (Hook.) L.E. Bishop, #197, Ranker & al., 2004, AY460622, AY459456, *Rojas 3233* (INB), Costa Rica, EF463804; *Chrysogrammitis musgraviana* (Baker) Parris, #2663, Ranker & al., 2004, AY460624, AY459458, *Kessler 12570* (UC), Sabah, Malaysia, EF463805; *Cochlidium seminudum* (Willd.) Maxon, #205, Ranker & al., 2004, AY460627, AY459460, *Hill 29102A* (no voucher), Dominican Republic, EF463806; *Ctenopteris lasiostipes* (Mett.) Brownlie, #213, Ranker & al., 2004, AY460630, AY459463, *Hodel 1448* (UC), New Caledonia, EF463807; *C. nutans* J. Sm., #2664, Ranker & al., 2004, AY460631, AY459464, *Ranker 1765* (COLO), Papua New Guinea, EF463808; *C. repandula* Kuntze, #2665, Ranker & al., 2004, AY460633, AY459466, *Ranker 1767* (COLO), Papua New Guinea, EF463809; *Dictymia mckeei* Tindale, #3540, *Schneider s.n.* (E), in cultivation, EF463246, EF463492, EF463810; *Drynaria rigidula* (Sw.) Bedd., #3531, *Schneider 297* (Z), Malaysia, EF463247, EF463493, EF463811; *Enteromorpha parietina* (Klotzsch) L.E. Bishop, #2398, *Schuettpeitz 230* (DUKE), Ecuador, EF463248, EF463494, EF463812; *Goniophlebium formosanum* (Baker) Rödl-Linder, #3547, *Ranker 1998* (COLO), Taiwan, EF463249, EF463495, EF463813; *Grammitis ciliata* Col., #932, Ranker & al., 2004, AY460638, AY459470, *Smith 2615* (UC), New Zealand, EF463814; *G. conjunctisora* (Baker) C. Morton, #2667, Ranker & al., 2004, AY460680, AY459514, *Ranker 1758* (COLO), Papua New Guinea, EF463815; *G. deplanchei* (Baker) Copel., #226, Ranker & al., 2004, AY460639, AY459471, *Hodel 1450* (UC), New Caledonia, EF463816; *G. hookeri* (Brack.) Copel., #230, Ranker & al., 2004, AY460642, AY459473, *Ranker 1116* (COLO), Hawaii, U.S.A., EF463817; *G. parva* (Brause) Copel., #2668, Ranker & al., 2004, AY460644, AY459476, *Ranker 1763a* (COLO), Papua New Guinea, EF463818; *G. poeppigiana* (Mett.) Pic. Serm., #2077, Ranker & al., 2004, AY460647, AY459479, *Taylor 6072* (UC), Chile, EF463819; *G. tenella* Kaulf., #241, Ranker & al., 2003, AF468198, AF469773, *Ranker 1352* (COLO), Hawaii, U.S.A., EF463820; *Lellingeria apiculata* (Kunze ex Klotzsch) A.R. Sm. & R.C. Moran, #242, Ranker & al., 2004, AY362343, AY459480, *Salino 3009* (UC), Brazil, EF463821; *L. hirsuta* A.R. Sm. & R.C. Moran, #244, Ranker & al., 2004, AY460649, AY459482, *Rojas 3145* (CR), Costa Rica, EF463822; *L. schenckii* (Hieron.) A.R. Sm. & R.C. Moran, #2666, Ranker & al., 2004, AY460651, AY459483, *Salino 4538* (UC), Brazil, EF463823; *Lemmaphyllum microphyllum* C. Presl, #3534, *Ranker 2010* (COLO), Taiwan, EF463250,

## Appendix 1. Continued.

EF463496, EF463824; *Lepisorus longifolius* (Blume) Holttum, #3514, *Schneider s.n.* (GOET), in cultivation, EF463251, EF463497, EF463825; *Loxogramme abyssinica* (Baker) M.G. Price, #3471, *Rakotondrainibe 6711* (P), Grande Comore, EF463252, EF463498, EF463826; *Melpomene moniliformis* (Lag. ex Sw.) A.R. Sm. & R.C. Moran, #267, Ranker & al., 2004, AY460654, AY459486, *Moraga 446* (INB), Costa Rica, EF463827; *Microgramma bifrons* (Hook.) Lellinger, #927, Schneider & al., 2004d, AY362582, #3477, *van der Werff 18062* (UC), Peru, EF463499, EF463828; *Micropolypodium hyalinum* (Maxon) A.R. Sm., #284, Ranker & al., 2004, AY362344, AY459490, *Rojas 3210* (UC), Costa Rica, EF463829; *M. taenifolium* (Jenman) A.R. Sm., #288, Ranker & al., 2004, AY460658, AY459491, *Rojas 3007* (UC), Costa Rica, EF463830; *Microsorium grossum* (Langsd. & Fisch.) S.B. Andrews, #3481, Ranker 1941 (COLO), Moorea, EF463253, EF463500, EF463831; *M. varians* (Mett.) Hennispan & Hett., #NA, Schneider & al., 2004d, AY362566, #3475, *Schneider s.n.* (GOET), in cultivation, EF463501, EF463832; *Neochirolepis palmatopedata* (Baker) H. Christ, #NA, Schneider & al., 2004d, AY362567, #3560, *Schneider s.n.* (GOET), in cultivation, EF463502, EF463833; *Niphidium crassifolium* (L.) Lellinger, #2377, Schuettpelz 209 (DUKE), Ecuador, EF463254, EF463503, EF463834; *Pecluma eurybasis* (C. Chr.) M.G. Price, #3472, *Danton s.n.* (GOET), Juan Fernandez Islands, EF463255, EF463504, EF463835; *Phlebodium decumanum* (Willd.) J. Sm., #2384, Schuettpelz 216 (DUKE), Ecuador, EF463256, EF463505, EF463836; *Platyserium stemaria* (P. Beauv.) Desv., #3544, *Kreier s.n.* (GOET), in cultivation, EF463257, EF463506, EF463837; *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf., #565, Hasebe & al., 1995, U21152, #3476, *Danton s.n.* (UC), Juan Fernandez Islands, EF463507, EF463838; *P. polypodioides* (L.) E.G. Andrews & Windham, #827, Schneider & al., 2004d, AY362592, #2670, *Christenhusz 3813* (DUKE), North Carolina, U.S.A., EF463508, EF463839; *P. sanctae-rosei* (Maxon) ined., #3580, Schuettpelz 525 (GOET), in cultivation, EF463258, EF463509, EF463840; *Polypodium vulgare* L., #NA, Hirohara & al., 2000, AB044899, #3474, *Schneider s.n.* (GOET), Germany, EF463510, EF463841; *Prosaptia contigua* (G. Forst.) C. Presl, #293, Ranker & al., 2004, AY362345, AY459494, *Chiou 97-09-12-05* (TAIF), Taiwan, EF463842; *P. obliquata* (Blume) Mett., #296, Ranker & al., 2004, AY460661, AY459495, *Chiou 97-09-12-04* (TAIF), Taiwan, EF463843; *Pyrosia polydactylis* (Hance) Ching, #3546, Ranker 2080 (COLO), Taiwan, EF463259, EF463511, EF463844; *P. serpens* (G. Forst.) Ching, #3532, Ranker 1933 (COLO), Moorea, French Polynesia, EF463260, EF463512, EF463845; *Scleroglossum sulcatum* (Kuhn) Alderw., #1008, Ranker & al., 2004, AY460664, AY459497, *Flynn 6287* (UC), Pohnpei, Caroline Islands, EF463846; *Selliguea lanceolata* Fée, #3536, Munzinger 1253 (P), New Caledonia, EF463261, EF463513, EF463847; *S. plantaginea* Brack., #3535, Ranker 1897 (COLO), Tahiti, French Polynesia, EF463262, EF463514, EF463848; *Serpocaulon fraxinifolium* (Jacq.) A.R. Sm., #587, Schneider & al., 2002, AY096207, #2432, Schuettpelz 264 (DUKE), Ecuador, EF463515, EF463849; *S. triseriale* (Sw.) A.R. Sm., #3543, Jimenez 1994 (UC), Bolivia, EF463263, EF463516, EF463850; *Synammia intermedia* (Colla) G. Kunkel, #3473, *Danton s.n.* (UC), Juan Fernandez Islands, EF463264, EF463517, EF463851; *Terpsichore anfractuosa* (Kunze ex Klotzsch) B. León & A.R. Sm., #254, Ranker & al., 2004, AY460668, AY459501, *Rojas 3321* (INB), Costa Rica, EF463852; *T. eggertii* (Baker ex Hook.) A.R. Sm., #309, Ranker & al., 2003, AF468209, AF469785, *Hill 29109* (UC), Dominican Republic, EF463853; *T. semihirsuta* (Klotzsch) A.R. Sm., #328, Ranker & al., 2004, AY460676, AY459509, *León 3655* (USM), Peru, EF463854; *T. senilis* (Fée) A.R. Sm., #323, Schneider & al., 2002, AY096208, Ranker & al., 2004, AY459510, *Rojas 3196* (INB), Costa Rica, EF463855; *Thylacopteris papillosa* (Blume) J. Sm., #3530, Schneider & al., 2004a, AY459175, *Gravendeel 559* (L), Java, Indonesia, EF463518, EF463856; **Pteridaceae:** *Acrostichum danaeifolium* Langsd. & Fisch., #3663, Schuettpelz & al., 2007, EF452129, EF452008, EF452065; *Actiniopteris dimorpha* Pic. Serm., #3515, Schuettpelz & al., 2007, EF452130, EF452009, EF452066; *Adiantopsis radiata* (L.) Fée, #3313, Schuettpelz & al., 2007, EF452131, EF452010, EF452067; *Adiantum capillus-veneris* L., #NA, Wolf & al., 2003, AY178864, AY178864, AY178864; *A. malesianum* J. Ghatak, #2506, Schuettpelz & al., 2007, EF452132, EF452011, EF452068; *A. pedatum* L., #636, Hasebe & al., 1994, U05602, #2499, Schuettpelz & al., 2007, EF452012, EF452069; *A. peruvianum* Klotzsch, #2507, Schuettpelz & al., 2007, EF452133, EF452013, EF452070; *A. raddianum* C. Presl, #637, Wolf & al., 1994, U05906, #638, Wolf, 1997, U93840, Schuettpelz & al., 2007, EF452071; *A. tenerum* Sw., #2504, Schuettpelz & al., 2007, EF452134, EF452014, EF452072; *A. tetraphyllum* Humb. & Bonpl. ex Willd., #2505, Schuettpelz & al., 2007, EF452135, EF452015, EF452073; *Aleuritopteris argentea* (S.G. Gmel.) Fée, #3734, Schuettpelz & al., 2007, EF452137, EF452016, EF452074; *Anetium citrifolium* (L.) Splitz., #697, Crane & al., 1995, U21284, #3339, Schuettpelz & al., 2007, EF452017, EF452075; *Antrophyum latifolium* Blume, #3078, Schuettpelz & al., 2007, EF452138, EF452018, EF452076; *Argyrochosma limitanea* (Maxon) Windham, #3179, Schuettpelz & al., 2007, EF452139, EF452019, EF452077; *Astrolepis sinuata* (Lag. ex Sw.) D.M. Benham & Windham, #2955, Schuettpelz & al., 2007, EF452141, EF452021, EF452079; *Bommeria hispida* (Mett. ex Kuhn) Underw., #3174, Schuettpelz & al., 2007, EF452142, EF452022, EF452081; *Ceratopteris richardii* Brongn., #NA, Masuyama & al., 2002, AB059585, #1027, Pryer & al., 2004, AY612691, Schuettpelz & al., 2007, EF452082; *Cheilanthes alabamensis* (Buckley) Kunze, #2964, Schuettpelz & al., 2007, EF452143, EF452023, EF452083; *C. eatonii* Baker, #2968, Schuettpelz & al., 2007, EF452144, EF452024, EF452084; *Coniogramme fraxinea* (D. Don) Fée ex Diels, #653, Korall & al., 2006b, AM177359, Pryer & al., 2004, AY612693, Korall & al., 2006b, AM176470; *Cryptogramma crispa* (L.) R. Br. ex Hook., #2949, Schuettpelz & al., 2007, EF452148, EF452027, EF452087; *Doryopteris ludens* (Wall. ex Hook.) J. Sm., #3510, Schuettpelz & al., 2007, EF452150, EF452031, EF452092; *Eriosorus cheilantheoides* (Sw.) A.F. Tryon, #3767, Schuettpelz & al., 2007, EF452152, EF452034, EF452095; *Haplopteris elongata* (Sw.) E.H. Crane, #2546, Schuettpelz & al., 2007, EF452153, EF452035, EF452096; *Hecistopteris pumila* (Spreng.) J. Sm., #703, Crane & al., 1995, U21286, #3278, Schuettpelz & al., 2007, EF452036, EF452097; *Hemionitis palmata* L., #NA, Geiger & Ranker, unpublished, AY357708, #2557, Schuettpelz & al., 2007, EF452037, EF452098; *Jamesonia verticalis* Kunze, #3768, Schuettpelz & al., 2007, EF452155, EF452038, EF452099; *Llavea cordifolia* Lag., #660, Gastony & Rollo, 1995, U27726, #3021, Schuettpelz & al., 2007, EF452039, EF452100; *Mildella henryi* (H. Christ) C.C. Hall & Lellinger, #3513, Schuettpelz & al., 2007, EF452146, EF452025, EF452085; *Monogramma graminea* (Poir.) Schkuhr, #3548, Schuettpelz & al., 2007, EF452157, EF452040, EF452102; *Neurocallis praestantissima* Bory ex Fée, #3294, Schuettpelz & al., 2007, EF452158, EF452042, EF452104; *Notholaena aschenborniana* Klotzsch, #3183, Schuettpelz & al., 2007, EF452159, EF452043, EF452105; *Ochropteris pallens* (Sw.) J. Sm., #3558, Schuettpelz & al., 2007, EF452160, EF452044, EF452106; *Onychium japonicum* Blume, #663, Hasebe & al., 1994, U05641, #3463, Schuettpelz & al., 2007, EF452045, EF452107; *Paraceterach marantae* (L.) R.M. Tryon, #3736, Schuettpelz & al., 2007, EF452161, EF452046,

## Appendix 1. Continued.

EF452108; *Pellaea truncata* Goodd., #3137, Schuettpelz & al., 2007, EF452164, EF452048, EF452110; *P. viridis* (Forssk.) Prantl, #3555, Schuettpelz & al., 2007, EF452147, EF452026, EF452086, *Pentagramma triangularis* (Kaulf.) Yatsk., Windham & E. Wollenw., #3152, Schuettpelz & al., 2007, EF452165, EF452049, *Pityrogramma austroamericana* Domin, #2561, Schuettpelz & al., 2007, EF452166, EF452050, EF452112; *P. jamesonii* (Baker) Domin, #3769, Schuettpelz & al., 2007, EF452167, *Moran 7592* (NY), Ecuador, EF463519, EF463857; *Platzzoma microphyllum* R. Br., #NA, Nakazato & Gastony, 2003, AY168721, #669, Schuettpelz & al., 2007, EF452051, EF452113; *Polytaenium cajenense* (Desv.) Benedict, #704, Crane & al., 1995, U20934, #2379, Schuettpelz & al., 2007, EF452052, EF452114; *Pteris arborea* L., #3321, Schuettpelz & al., 2007, EF452168, EF452053, EF452116; *P. argyraea* T. Moore, #3597, Schuettpelz & al., 2007, EF452169, EF452054, EF452117; *P. cretica* L., #3644, Schuettpelz & al., 2007, EF452170, EF452055, EF452118; *P. multifida* Poir., #3640, Schuettpelz & al., 2007, EF452171, EF452056, EF452119; *P. propinqua* J. Agardh, #2436, Schuettpelz & al., 2007, EF452172, EF452057, EF452120; *P. quadriaurita* Retz., #3601, Schuettpelz & al., 2007, EF452173, EF452058, EF452121; *P. tremula* R. Br., #3667, Schuettpelz & al., 2007, EF452174, EF452059, EF452122; *P. vittata* L., #671, Wolf & al., 1994, U05941, #3400, Schuettpelz & al., 2007, EF452060, EF452123; *Pterozonium brevifrons* (A.C. Sm.) Lellinger, #2453, Schuettpelz & al., 2007, EF452175, EF452061, EF452124; *Radiovittaria gardneriana* (Fée) E.H. Crane, #707, Crane & al., 1995, U21294, #2417, Schuettpelz & al., 2007, EF452062, EF452125; *Vittaria graminifolia* Kaulf., #715, Crane & al., 1995, U21295, #2395, Schuettpelz & al., 2007, EF452064, EF452128; **Saccolomataceae:** *Saccoloma inaequalis* (Kunze) Mett., #3419, *Christenhusz 4233* (TUR), Puerto Rico, EF463265, EF463520, EF463858; **Salviniaceae:** *Azolla pinnata* R. Br., #2113, Korall & al., 2006b, AM177355, #2023, Korall & al., 2006b, AM176622, *Schneider s.n.* (GOET), in cultivation, EF463859; *Salvinia cucullata* Roxb., #674, Hasebe & al., 1994, U05649, #2028, *Schneider s.n.* (GOET), in cultivation, EF463521, EF463860; **Schizaeaceae:** *Schizaea dichotoma* (L.) J. Sm., #NA, Wikström & al., 2002, AJ303408, #679, Pryer & al., 2004, AY612709, *Game 98/07* (UC), Cook Islands, EF463861; **Tectariaceae:** *Arthropteris parallela* C. Chr., #3579, *Schuettpelz 524* (GOET), in cultivation, EF463266, EF463522, EF463862; *Heterogonium pinnatum* (Copel.) Holttum, #3610, *Schuettpelz 555* (GOET), in cultivation, EF463267, EF463523, EF463863; *Psammisorus paucivenius* C. Chr., #3539, *Rakotondrainibe 6585* (P), Madagascar, EF463268, EF463524, EF463864; *Tectaria antioquoiana* (Baker) C. Chr., #2368, *Schuettpelz 200* (DUKE), Ecuador, EF463269, EF463525, EF463865; *T. apifolia* (Schkuhr) Copel., #3056, *Christenhusz 3201* (IJ), Jamaica, EF463270, EF463526, EF463866; *T. fimbriata* (Willd.) Proctor & Lourteig, #3527, *Christenhusz 3537* (TUR), Puerto Rico, EF463271, EF463527, EF463867; *T. incisa* Cav., #3057, *Christenhusz 3209* (IJ), Jamaica, EF463272, EF463528, EF463868; *T. prolifera* (Hook.) R.M. Tryon & A.F. Tryon, #3058, *Christenhusz 3368* (IJ), Jamaica, EF463273, EF463529, EF463869; *T. trifoliata* (L.) Cav., #3302, *Christenhusz 4013* (TUR), Guadeloupe, EF463274, EF463530, EF463870; *T. zeylanica* (Houtt.) Sledge, #3569, *Schuettpelz 514* (GOET), in cultivation, EF463275, EF463531, EF463871; *Triplophyllum funestum* (Kunze) Holttum, #3359, *Christenhusz 4107* (TUR), Guadeloupe, EF463276, EF463532, EF463872; **Thelypteridaceae:** *Macrothelypteris torresiana* (Gaud.) Ching, #2980, *Schuettpelz 335* (DUKE), in cultivation, EF463277, EF463533, EF463873; *Phegopteris hexagonoptera* (Michx.) Fée, #2731, *Christenhusz 3844* (DUKE), South Carolina, U.S.A., EF463278, EF463534, EF463874; *Pseudophegopteris cruciata* (Willd.) Holttum, #3559, *Janssen 2724* (P), Reunion, EF463279, EF463535, EF463875; *Thelypteris abrupta* (Desv.) Proctor, #3286, *Christenhusz 3985* (TUR), Guadeloupe, EF463280, EF463536, EF463876; *T. affine* (Blume) ined., #3626, *Schuettpelz 572* (GOET), in cultivation, EF463281, EF463537, EF463877; *T. clypeolulata* (Desv.) Proctor, #3303, *Christenhusz 4017* (TUR), Guadeloupe, EF463282, EF463538, EF463878; *T. consanguinea* (Fée) Proctor, #3325, *Christenhusz 4060* (TUR), Guadeloupe, EF463283, EF463539, EF463879; *T. dentata* (Forssk.) E.P. St. John, #3654, *Schuettpelz 607* (B), in cultivation, EF463284, EF463540, EF463880; *T. gemmulifera* (Hieron.) A.R. Sm., #3747, *Huiet s.n.* (UC), in cultivation, EF463285, EF463541, EF463881; *T. glandulosa* (Desv.) Proctor, #3343, *Christenhusz 4083* (TUR), Guadeloupe, EF463286, EF463542, EF463882; *T. globulifera* (Brack.) C.F. Reed, #3773, *Game s.n.* (UC), Hawaii, U.S.A., EF463287, EF463543, EF463883; *T. gracilis* (Heward) Proctor, #3392, *Christenhusz 4182* (TUR), Guadeloupe, EF463288, EF463544, EF463884; *T. limbosperma* (All.) H.P. Fuchs, #3565, *Christenhusz 3719* (TUR), Scotland, U.K., EF463289, EF463545, EF463885; *T. linkiana* (C. Presl) R.M. Tryon, #3393, *Christenhusz 4185* (TUR), Guadeloupe, EF463290, EF463546, EF463886; *T. longissima* (Brack.) C.F. Reed, #3775, *Game 99/270* (UC), Fiji, EF463291, EF463547, EF463887; *T. meniscioides* (Liebm.) C.F. Reed, #3743, *Huiet s.n.* (UC), in cultivation, EF463292, EF463548, EF463888; *T. noveboracensis* (L.) Nieuwland, #2725, *Christenhusz 3831* (DUKE), Georgia, U.S.A., EF463293, EF463549, EF463889; *T. oligocarpa* (Humb. & Bonpl. ex Willd.) Ching, #693, *Chisaki 1000* (UC), Costa Rica, EF463294, EF463550, EF463890; *T. opulenta* (Kaulf.) Fosberg, #3612, *Schuettpelz 557* (GOET), in cultivation, EF463295, EF463551, EF463891; *T. ovata* R.P. St. John, #2972, *Schuettpelz 327* (DUKE), in cultivation, EF463296, EF463552, EF463892; *T. palustris* (Salisb.) Schott, #694, Wolf & al., 1994, U05947, Pryer & al., 2004, AY612713, Schuettpelz & al., 2007, EF452127; *T. poiteana* (Bory) Proctor, #1235, *Mickel 5799* (NY), Oaxaca, Mexico, EF463297, EF463553, EF463893; *T. reticulata* (L.) Proctor, #3362, *Christenhusz 4112* (TUR), Guadeloupe, EF463298, EF463554, EF463894; *T. rustica* (Fée) Proctor, #3390, *Christenhusz 4180* (TUR), Guadeloupe, EF463299, EF463555, EF463895; *T. seemanii* (Holttum) ined., #3774, *Game 95/147* (UC), Fiji, EF463300, EF463556, EF463896; *T. simplex* (Hook.) K. Iwats., #1075, *Bartholomew 573* (UC), Hong Kong, EF463301, EF463557, EF463897; *T. sp.*, #3549, *Janssen 2679* (P), Reunion, EF463303, EF463559, EF463899; *T. tylodes* (Kunze) Ching, #3698, *Olsen s.n.* (no voucher), in cultivation, EF463302, EF463558, EF463898; **Thyrsopteridaceae:** *Thyrsopteris elegans* Kunze, #2477, Korall & al., 2006b, AM177353, AM176620, *Morter 18* (E), in cultivation, EF463900; **Woodsiaceae:** *Athyrium distentifolium* Tausch ex Opiz, #3581, *Schuettpelz 526* (GOET), in cultivation, EF463304, EF463560, EF463901; *A. filix-femina* (L.) Roth, #26, Wolf & al., 1994, U05908, #2669, *Christenhusz 3814* (DUKE), North Carolina, U.S.A., EF463561, EF463902; *A. niponicum* (Mett.) Hance, #27, Sano & al., 2000, D43891, #2852, *Kato s.n.* (no voucher), Japan, EF463562, EF463903; *A. otophorum* (Miq.) Koidz., #3744, *Smith s.n.* (UC), in cultivation, EF463305, EF463563, EF463904; *A. yokoscense* (Franch. & Sav.) H. Christ, #30, Sano & al., 2000, D43893, #2853, *Kato s.n.* (no voucher), in cultivation, EF463564, EF463905; *Cornopteris decurrenti-alata* (Hook.) Nakai, #31, Sano & al., 2000, D43897, #2854, *Kato s.n.* (no voucher), in cultivation, EF463565, EF463906; *Cystopteris reevesiana* Lellinger, #3126, Schuettpelz & al., 2007, EF452149, EF452028, EF452088; *Deparia bonincola* (Nakai) M. Kato, #NA, Sano & al., 2000, D43899, #2860, *Kato s.n.* (no voucher), in cultivation, EF463566, EF463907; *D. lancea* (Thunb.) Fraser-Jenk., #2558, *Schuettpelz 298* (DUKE), in cul-

## Appendix 1. Continued.

tivation, EF463306, EF463567, EF463908; *D. petersenii* (Kunze) M. Kato, #NA, Shinohara & al., 2003, AB095978, #2864, *Kato s.n.* (no voucher), in cultivation, EF463568, EF463909; *D. unifurcata* (Baker) M. Kato, #2865, *Kato s.n.* (no voucher), in cultivation, EF463307, EF463569, EF463910; *Diplazium bombonae* Rosenst., #3764, *Moran 7493* (NY), Ecuador, EF463308, EF463570, EF463911; *D. centripetale* (Baker) Maxon, #3421, *Christenhusz 4236* (UPR), Puerto Rico, EF463309, EF463571, EF463912; *D. cristatum* (Desr.) Alston, #3310, *Christenhusz 4029* (TUR), Guadeloupe, EF463310, EF463572, EF463913; *D. dilatatum* Blume, #3638, *Schuettpelez 588* (GOET), in cultivation, EF463311, EF463573, EF463914; *D. hachijoense* Nakai, #2868, *Kato s.n.* (no voucher), in cultivation, EF463312, EF463574, EF463915; *D. legalloi* Proctor, #3328, *Christenhusz 4063* (TUR), Guadeloupe, EF463313, EF463575, EF463916; *D. plantaginifolium* (L.) Urb., #3305, *Christenhusz 4019* (TUR), Guadeloupe, EF463314, EF463576, EF463917; *D. proliferum* (Lam.) Thouars, #3639, *Schuettpelez 590* (GOET), in cultivation, EF463315, EF463577, EF463918; *D. virescens* Kunze, #2873, *Kato s.n.* (no voucher), in cultivation, EF463316, EF463578, EF463919; *D. wichurae* (Mett.) Diels, #NA, Yatabe & al., unpublished, AB042744, #2874, *Kato s.n.* (no voucher), in cultivation, EF463579, EF463920; *Gymnocarpium dryopteris* (L.) Newman, #3066, *Yatskievych 02-31* (DUKE), Yunnan, China, EF463317, EF463580, EF463921; *Hemidictyum marginatum* (L.) C. Presl, #3054, *Christenhusz 2476* (CAY), French Guiana, EF463318, EF463581, EF463922; *Woodsia obtusa* (Spreng.) Torr., #2973, *Schuettpelez 328* (DUKE), in cultivation, EF463319, EF463582, EF463923.

## Appendix 2. Amplification and sequencing primers routinely used in this study of leptosporangiate fern phylogeny.

Primer	Use <sup>a</sup>	Sequence (5' to 3')	Reference
<i>rbcL</i>			
AF	FA	ATGTCACCACAAACAGAGACTAAAGC	Hasebe & al., 1994
ESRBCL1F	FA*	ATGTCACCACAAACGGAGACTAAAGC	This study
ESRBCL628F	FS*	CCATTYATGCGTTGGAGAGATCG	This study
ESRBCL645F	FS	AGAYCGTTTCYTATTYGTAGCAGAAGC	This study
ESRBCL654R	RS*	GAARCGATCTCTCCAACGCAT	This study
ESRBCL663R	RS	TACRAATARGAAACGRTCTCTCCAACG	This study
ESRBCL1361R	RA*	TCAGGACTCCACTACTAGCTTCACG	This study
1379R	RA	TCACAAGCAGCAGCTAGTTCAGGACTC	Pryer & al., 2001b
<i>atpB</i>			
ESATPB172F	FA*	AATGTTACTTGTGAAGTWCAACAAT	This study
ESATPB221F	FA	GCCGTRGCTATGAGTGCCACAGA	This study
ATPB672F	FA	TTGATACGGGAGCYCCTCTWAGTGT	Wolf, 1997
ATPB493F	FS	GGATCTTTTGGCCGTATCGTCG	Pryer & al., 2004
ATPB609R	RS	TCRTTDCCTTCRCGTGTACGTTT	Pryer & al., 2004
ESATPB701F	FS	TATGGTCAGATGAATGAACC	This study
ATPB1163F	FS*	ATGGCAGAATRTTCCGAGATRTYA	Wolf, 1997
ESATPB912R	RS	ATTTCTGTACCAAGRGTCGGTTG	This study
ATPB910R	RS*	TTCTGTYARAGANCCCATTTCTGT	Pryer & al., 2004
ATPB1419F	FS	CRACATTTGCACATYTRGATGCTAC	Wolf, 1997
ATPB1592R	RS	TGTAACGYTYAAAAGTTTGCTTAA	Wolf, 1997
ESATPE45R	RA*	ATTCCAAACWATTCGATTWGGAG	This study
ESATPE47R	RA	GAATTCCAAACWATTCGATTAGGAG	This study
ATPE384R	RA	GAATTCCAAACTATTTCGATTAGG	Pryer & al., 2004
<i>atpA</i>			
ESATPF412F	FA*	GARCARGTTCGACAGCAAGT	Schuettpelez & al., 2006
ESATPF415F	FA	CARGTTCGACAGCAAGTYTCTCG	Schuettpelez & al., 2006
ESATPA283F	FS	GGYAAAGATTGCTCAAATACCAG	Schuettpelez & al., 2006
ESATPA535F	FS*	ACAGCAGTAGCTACAGATAC	Schuettpelez & al., 2006
ESATPA557R	RS*	ATTGTATCTGTAGCTACTGC	Schuettpelez & al., 2006
ESATPA787F	FS	TACGACGATCTYTCTAAACAAGC	Schuettpelez & al., 2006
ESATPA823R	RS	GTCGATAAGCYTGAGCTTGTTAG	Schuettpelez & al., 2006
ESATPA856F	FS*	CGAGAAGCATATCCGGGAGATG	Schuettpelez & al., 2006
ESATPA877R	RS*	CATCTCCCGGATATGCTTCTCG	Schuettpelez & al., 2006
ESTRNR46F	RA*	GTATAGGTTTCRARTCTATTGGACG	Schuettpelez & al., 2006

<sup>a</sup>F, forward; R, reverse; A, amplification and sequencing; S, sequencing only; \*, most commonly used.