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Fern classification

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16.1 Introduction and historical summary

Over the past 70 years, many fern classifications, nearly all based on morphology, most explicitly or implicitly phylogenetic, have been proposed. The most complete and commonly used classifications, some intended primarily as herbarium (filing) schemes, are summarized in Table 16.1, and include: Christensen (1938), Copeland (1947), Holttum (1947, 1949), Nayar (1970), Bierhorst (1971), Crabbe *et al.* (1975), Pichi Sermolli (1977), Ching (1978), Tryon and Tryon (1982), Kramer (in Kubitzki, 1990), Hennipman (1996), and Stevenson and Loconte (1996). Other classifications or trees implying relationships, some with a regional focus, include Bower (1926), Ching (1940), Dickason (1946), Wagner (1969), Tagawa and Iwatsuki (1972), Holttum (1973), and Mickel (1974). Tryon (1952) and Pichi Sermolli (1973) reviewed and reproduced many of these and still earlier classifications, and Pichi Sermolli (1970, 1981, 1982, 1986) also summarized information on family names of ferns. Smith (1996) provided a summary and discussion of recent classifications.

With the advent of cladistic methods and molecular sequencing techniques, there has been an increased interest in classifications reflecting evolutionary relationships. Phylogenetic studies robustly support a basal dichotomy within vascular plants, separating the lycophytes (less than 1% of extant vascular plants) from the euphyllophytes (Figure 16.1; Raubeson and Jansen, 1992, Kenrick and Crane, 1997; Pryer *et al.*, 2001a, 2004a, 2004b; Qiu *et al.*, 2006). Living euphyllophytes, in turn, comprise two major clades: spermatophytes (seed plants), which are in excess of 260 000 species (Thorne, 2002; Scotland and Wortley,

The Biology and Evolution of Ferns and Lycophytes, ed. Tom A. Ranker and Christopher H. Haufler.
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Table 16.1 Comparison of fern classifications relative to Smith et al., 2006b.

+, indicates a circumscription the same as, or essentially the same as, the one adopted by Smith et al. (2006b); -, indicates a family with different circumscription than in Smith et al. (2006b); 0, family not recognized, i.e., included in another family, either implicitly or explicitly; ?, no mention of family (family not treated), or circumscription unclear. The last row gives percentages of classifications, for a given family, with the same circumscription as Smith et al. (2006b) and excluding those classifications for which there is doubt, or no mention (?) of circumscription. Oph, Ophioglossaceae; Psi, Psilotaceae; Equ, Equisetaceae; Mar, Marattiaceae; Osm, Osmundaceae; Hym, Hymenophyllaceae; Gle, Gleicheniaceae; Dip, Dipteridaceae; Mat, Matoniaceae; Lyg, Lygodiaceae; Ane, Anemiaceae; Sch, Schizaeaceae; Mrs, Marsileaceae; Sal, Salviniaceae; Thy, Thyrsopteridaceae; Lox, Loxomataceae; Cul, Culcitaceae; Pla, Plagiogyriaceae; Cib, Cibotiaceae; Cya, Cyatheaceae; Dic, Dicksoniaceae; Met, Metaxyaceae; Lin, Lindsaeaceae; Sac, Saccolomataceae; Den, Dennstaedtiaceae; Pte, Pteridaceae; Asp, Aspleniaceae; The, Thelypteridaceae; Woo, Woodsiaceae; Ble, Blechnaceae; Ono, Onocleaceae; Dry, Dryopteridaceae; Lom, Lomaropsidiaceae; Tec, Tectariaceae; Ole, Oleandraceae; Dav, Davalliaceae; Pol, Polypodiaceae.

	Oph	Psi	Equ	Mar	Osm	Hym	Gle	Dip	Mat	Lyg	Ane	Sch	Mrs	Sal	Thy	Lox	Cul	Pla	Cib	Cya	Dic	Met	Lin	Sac	Den	Pte	Asp	The	Woo	Ble	Ono	Dry	Lom	Tec	Ole	Dav	Pol			
Bierhorst, 1971	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Ching, 1978	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Christensen, 1938	+	?	?	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Copeland, 1947	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Crabbe et al., 1975	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Hennipman, 1996	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Holtum, 1947, 1949	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kubitzki, 1990	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Nayar, 1970	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pichi Sermolli, 1977	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Smith et al., 2006a	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Stevenson and Leconte, 1996	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Tryon and Tryon, 1982	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
% agreement with Smith et al., 2006b	73	75	100	45	92	92	42	11	90	33	27	27	90	27	9	80	9	92	0	8	0	45	25	0	8	17	75	67	0	67	17	0	0	0	0	17	0	0	25	

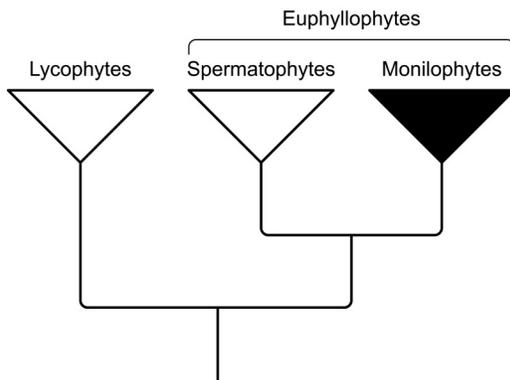


Figure 16.1 Consensus phylogeny depicting relationships of major vascular plant lineages. The topology summarizes the results of previously published phylogenetic studies (e.g., Raubeson and Jansen, 1992; Kenrick and Crane, 1997; Renzaglia *et al.*, 2000; Pryer *et al.*, 2001a; see main text for others). Resolved nodes have received bootstrap support ≥ 70 (From Smith *et al.*, 2006b).

2003), and ferns (*sensu* Pryer *et al.*, 2004b), with about 9000 species, including horsetails, whisk ferns, and all eusporangiate and leptosporangiate ferns. Based on current evidence, extant ferns appear to be a monophyletic group characterized by lateral root origin in the endodermis, usually mesarch protoxylem in shoots, a pseudoendospore, plasmodial tapetum, and sperm cells with 30–1000 flagella (Renzaglia *et al.*, 2000; Schneider *et al.*, 2002a). Plants in the lycophyte and fern clades are all spore bearing or “seed-free,” and because of this common feature their members have been lumped together historically under various terms, such as “pteridophytes” and “ferns and fern allies” – paraphyletic assemblages of plants.

Ideally, morphological data from fossils should also be used in constructing classifications, but this has generally not been done for ferns, except at higher levels in the hierarchy (e.g., by Kenrick and Crane, 1997). Rothwell and Nixon (2006) argued that the addition of fossil data in phylogenetic analyses can alter the topologies of trees obtained using data from only extant species. However, trees produced by adding selected fossil taxa to morphological and/or molecular data sets containing extant species (e.g., Fig. 4B in Rothwell and Nixon, 2006) are often poorly resolved. Although trees based only on morphological data from fossils and extant taxa (e.g., Rothwell, 1999) differ in many respects from phylogenetic hypotheses based on morphological and molecular data, or from hypotheses based only on molecular data, they do provide perspectives that may provide useful alternative hypotheses. Many factors contribute to the lack of resolution in trees containing fossils including: (1) the paucity of extinct taxa

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that successfully fossilized; (2) our inability to find (or recognize) crucial fossils that aid in filling evolutionary gaps; (3) the low proportion of phylogenetically informative characters, in both gametophytic and sporophytic phases, that are assessable in most fossils; (4) the incompleteness or fractured nature of most fossil taxa; and (5) the inherent difficulty of scoring morphological characters, which in turn may be due to considerable morphological homoplasy in ferns (Ranker *et al.*, 2004). All of these features make the incorporation of fossil data into matrices containing data from extant plants challenging. Fossil data can be used to pinpoint divergence times of lineages (Lovis, 1977; Pryer *et al.*, 2004b; Schneider *et al.*, 2004c) and as the quality and abundance of fossil evidence for ferns improve, fossil data will aid in building even more robust phylogenies. This, in turn, may provide reciprocal illumination for understanding the evolution of characters and character states of extant taxa. Because we consider it impractical at present to include fossil data in taxonomically diverse datasets, in this chapter we develop a classification based solely on morphological and molecular data from extant species.

16.2 Review of critical recent advances

Molecular phylogenetic hypotheses for extant ferns (see Chapter 15) have utilized data from several chloroplast markers (*rbcl*, *atpA*, *atpB*, *accD*, *rps4*, 16S rDNA, ITS), one nuclear gene (18S rDNA), and three mitochondrial genes (*atp1*, *nad2*, *nad5*). A natural outgrowth of these one-gene or few-gene studies on a wide array of ferns has led to still broader, and increasingly robust multiple-gene phylogenetic analyses, e.g., studies by Wolf (1996b), Wolf *et al.* (1998), Pryer *et al.* (2001a, 2004b), Schneider *et al.* (2004c), Wikström and Pryer (2005), Schuettpelz *et al.* (2006), and Schuettpelz and Pryer (in press). A multiple-gene analysis examining the relationships of all land plants (Qiu *et al.*, 2006) has largely confirmed the basic relationships uncovered in the fern studies. Attempts to generate morphologically based phylogenetic hypotheses for ferns are far fewer (Pryer *et al.* 1996, 2001a; Schneider, 1996a; Stevenson and Loconte, 1996; Rothwell, 1999; Schneider *et al.*, in preparation), perhaps because of the inherent difficulties in defining characters and assessing characters states, but at least in some cases this approach has added support for molecular-based consensus phylogenies.

All of these studies have given rise to growing confidence in relationships and correspondingly to the composition of taxa at familial and ordinal ranks. This convinced us that it was timely to attempt a reclassification of extant ferns (Smith *et al.*, 2006b). In that paper, the classificatory decisions/innovations reflect a growing reliance on a solid phylogenetic underpinning for the development of useful multipurpose classifications. As in that publication, we focus on the

ranks of class, order, and family. We assert that the information available is most appropriate for resolution and understanding of relationships at these levels, and that within most families, especially at the generic level, there is still insufficient evidence to attempt many classificatory decisions. Only one previous fern classification has employed cladistic methodology in a rigorous way; Stevenson and Loconte (1996) superimposed on their tree a hierarchical classification, but the phylogeny that they generated as a basis for their classification was based exclusively on morphological data and differs radically from the most up-to-date phylogenetic hypotheses. Our classification, in contrast, is based on consensus of a variety of morphological and molecular studies.

The impact of molecular phylogenetic studies on classification will likely continue, perhaps at an accelerated rate. Already, since our recent reclassification (Smith *et al.*, 2006b), several additional phylogenetic studies have been published or are in press, e.g., for the Cyatheales (Korall *et al.*, 2006a, 2006b, 2007), Dryopteridaceae and related families (Li and Lu, 2006; Lu and Li, 2006; Tsutsumi and Kato, 2006), Hymenophyllaceae (Ebihara *et al.*, 2006; Hennequin *et al.*, 2006a, 2006b), Marsileaceae (Nagalingum *et al.*, 2006, 2007), Pteridaceae (Schuettpezel *et al.*, 2007), and Salviniaceae (Metzgar *et al.*, in press). These generally reinforce decisions made in our previous paper, and largely confirm the higher level (order and family) structure of the classification (Schuettpezel *et al.*, 2006; Schuettpezel and Pryer, in press) or suggest the recognition or rejection of taxa at generic level.

16.3 Synthesis of current perspectives: the classification of ferns

In our reclassification (Smith *et al.*, 2006b), we combined the principle of monophyly with a decision to maintain well-established names to update ordinal and familial ranks within ferns so that they are better reconciled with our current best estimates of phylogenetic relationships. We utilized a minimum number of ranks to categorize only the most well-supported splits in the phylogeny, and we treat all classes, orders, and families of extant ferns, which constitute a monophyletic group, sometimes called Infradivision Moniliformopses (Kenrick and Crane, 1997), or monilophytes (Pryer *et al.*, 2001a, 2004a, 2004b; Donoghue in Judd *et al.*, 2002). However, “Infradivision” is not a recognized rank in the International Code of Botanical Nomenclature (Greuter *et al.*, 2000); moreover, the name “Moniliformopses” was never validly published, lacking a Latin diagnosis or description, or a reference to one. Because validly published names for ferns (as we define them) at ranks above class are either not available or have been interpreted in a manner we think might be confusing or incompatible with current hypotheses of relationship, we avoid their use.

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For each family, we provide important heterotypic synonyms, approximate numbers of genera and species, names of constituent genera, references to relevant phylogenetic literature, and, where appropriate, discussion of unresolved problems. DNA sequence data are now available for all families we recognize, and for most genera of ferns. A superscript number one (¹) denotes those genera for which DNA sequence data are not available; nonetheless, taxonomic placement for most of these is relatively certain, based on morphological evidence. Lack of a superscript indicates that some molecular evidence (either published or unpublished) has been available to us for consideration. The classification presented below is based on the consensus relationships depicted in Chapter 15, which are derived from, and guided by, recent and ongoing phylogenetic studies.

Fern names at family rank used in this classification were obtained from the website of James Reveal, University of Maryland (www.life.umd.edu/emeritus/reveal/PBIO/fam/hightaxaindex.html) and from Hoogland and Reveal (2005); all family names, and cross-references if any, are listed in Appendix A. Most names at family rank are also listed and discussed by Pichi Sermolli (1970, 1982) and summarized in reports by the Subcommittee for Family Names of Pteridophyta (Pichi Sermolli, 1981, 1986); this list was further emended and updated by Pichi Sermolli (1993). Names at ordinal, supraordinal, and subordinal ranks are also available from the Reveal website and from Hoogland and Reveal (2005) (see Appendices 1 and 2 in Smith *et al.*, 2006b); literature citations for all names were given by Smith *et al.* (2006b, Appendix 4). At the end of this chapter, we give an index to commonly accepted genera with family assignments proposed here (Appendix B).

Within ferns, we recognize four classes (Psilotopsida, Equisetopsida, Marattiopsida, Polypodiopsida), 11 orders, and 37 families.

I. Class Psilotopsida

A. Order Ophioglossales

1. **Family Ophioglossaceae** (incl. Botrychiaceae, Helminthostachyaceae). Four genera: *Botrychium* (grapeferns, moonworts), *Helminthostachys*, *Mankyua*¹, *Ophioglossum* (adder tongues); *Botrychium* (incl. *Botrychium s.s.*, *Sceptridium*, *Botrypus*, and *Japanobotrychium*) and *Ophioglossum* (incl. *Cheiroglossa*, *Ophioderma*) are sometimes divided more finely (Kato, 1987; Hauk *et al.*, 2003). Ca. 80 species; monophyletic (Hasebe *et al.*, 1996; Hauk, 1996; Pryer *et al.*, 2001a, 2004b; Hauk *et al.*, 2003). *Mankyua*, from Cheju Island, Korea, has recently been described, but no molecular data are available (Sun *et al.*, 2001). Non-coding chloroplast genes recover similar topologies as coding genes in *Botrychium s.l.* (Small *et al.*, 2005).

Species mostly terrestrial (a few epiphytic), temperate and boreal, but a few pantropical. Characters: veneration nodding (not circinate); rhizomes and petioles fleshy; root hairs lacking; aerophores absent (Davies, 1991); fertile leaves each with a single sporophore arising at the base of, or along, the trophophore stalk, or at the base of the trophophore blade (several sporophores per blade in *Cheiroglossa*); sporangia large, with walls two cells thick, lacking an annulus; spores globose-tetrahedral, trilete, many (>1000) per sporangium; gametophytes subterranean, non-photosynthetic, mycorrhizal; $x = 45$ (46).

B. *Order Psilotales*

2. **Family Psilotaceae** (whisk ferns; incl. Tmesipteridaceae). Two genera (*Psilotum*, *Tmesipteris*), ca. 12 species total (two in *Psilotum*); monophyletic (Hasebe *et al.*, 1996; Pryer *et al.*, 2001a, 2004b). Characters: roots absent; stems bearing reduced, unveined or single-veined euphylls; sporangia large, with walls two cells thick, lacking an annulus; two or three sporangia fused to form a synangium, seemingly borne on the adaxial side of a forked leaf; spores reniform, monolete, many (>1000) per sporangium; gametophytes subterranean (*Psilotum*), non-photosynthetic, mycorrhizal; $x = 52$.

II. *Class Equisetopsida* [= *Sphenopsida*]

C. *Order Equisetales*

3. **Family Equisetaceae** (horsetails). A single genus (*Equisetum*), 15 species usually placed in two well-marked subgenera, subg. *Equisetum* and subg. *Hippochaete*; monophyletic (Pryer *et al.*, 2001a, 2004b; Des Marais *et al.*, 2003; Guillon, 2004). The spermatozoids of *Equisetum* share several important features with other ferns that support their inclusion in this clade (Renzaglia *et al.*, 2000). Kato (1983) adduced additional morphological characters, including root characters, supporting a relationship between horsetails and ferns. Characters: stems with whorled branching, lacunate; leaves whorled, connate; sporangia with helical secondary wall thickenings (Bateman, 1991), borne on peltate sporangiophores that collectively comprise strobili; sporangia large, lacking an annulus, many (>1000) per sporangium; spores green, with circular aperture and four paddle-like, coiled elaters; gametophytes green, surficial; $x = 108$.

III. *Class Marattiopsida*

D. *Order Marattiales* (incl. *Christenseniales*)

4. **Family Marattiaceae** (marattioids; incl. Angiopteridaceae, Christenseniaceae, Danaeaceae, Kaulfussiaceae). Four genera: *Angiopteris*, *Christensenia*, *Danaea*, *Marattia*. As currently circumscribed, *Marattia* is paraphyletic, and will be

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subdivided into three elements, one requiring a new generic name (A. G. Murdock, personal communication). *Archangiopteris* has been recognized by some (e.g., Pichi Sermolli, 1977) but appears to nest within *Angiopteris* (Murdock, 2005, personal communication). *Danaea* is sister to the other three genera (Pryer *et al.* 2001a; 2004b; Murdock, 2005) and represents a neotropical radiation (Christenhusz *et al.*, in review). *Angiopteris* and *Christensenia* are restricted to eastern and southeastern Asia, Australasia, and Polynesia, while *Marattia s.l.* is pantropical. Ca. 150 species, but monographic revision is needed at the species level in several genera; monophyletic (Hill and Camus, 1986; Pryer *et al.*, 2001a, 2004b; Murdock, 2005). We see no advantage or good reason for recognizing several of the constituent genera as monogeneric families, as done by Pichi Sermolli (1977), and the paraphyly of *Marattia vis-a-vis Angiopteris*, necessitating a recircumscription of marattioid genera (A. G. Murdock, personal communication), reinforces this opinion. The name Danaeaceae has been found to predate Marattiaceae; however, Marattiaceae has been proposed for conservation by Murdock *et al.* (2006), and we maintain its usage in the usual broad sense.

Terrestrial (rarely epipetric) pantropical, fossils beginning in Carboniferous (Collinson, 1996). Characters: roots large, fleshy, with polyarch xylem; root hairs septate; roots, stems, and leaves with mucilage canals; rhizomes fleshy, short, upright or creeping, with a polycyclic dictyostele; vernation circinate; leaves large, fleshy, 1–3-pinnate (rarely simple in *Danaea*, or 3–5-foliolate in *Christensenia*) with enlarged, fleshy, starchy stipules at the base and swollen pulvinae along petioles and rachises (and sometimes other axes); petiole and stem xylem polycyclic; stems and blades bearing scales; pneumathodes (lenticels) scattered all around petioles and/or rachises; sporangia free or in round or elongate synangia (fused sporangia), lacking an annulus, enclosing 1000–7000 spores; spores usually bilateral or ellipsoid, monolete; gametophytes green, surficial; $x = 40$ (39).

IV. Class Polypodiopsida [= Filicopsida]

E. Order Osmundales

5. Family Osmundaceae. Four genera: *Leptopteris*, *Osmunda*, *Osmundastrum*, *Todea*. Ca. 20 species; monophyletic (Hasebe *et al.*, 1996; Yatabe *et al.*, 1999; Pryer *et al.*, 2001a, 2004b). Evidence from morphology (Miller, 1971) and molecules (Yatabe *et al.*, 1999) suggests that *Osmundastrum cinnamomea* (L.) C. Presl be recognized as an independent, monotypic genus (Yatabe *et al.*, 2005); there is support for three subgenera within *Osmunda s.s.*: subg. *Osmunda*, subg. *Claytosmunda* Y. Yatabe *et al.*, and subg. *Plenasium* (C. Presl) Milde. Fossils from Permian; temperate and tropical. Characters: stem anatomy distinctive, an ectophloic siphonostele, with

a ring of discrete xylem strands, these often conduplicate or twice conduplicate in cross-section; stipules at bases of petioles; leaves dimorphic or with fertile portions dissimilar to sterile; sporangia large, with 128–512 spores, opening by an apical slit, annulus lateral; spores green, subglobose, trilete; gametophytes large, green, cordate, surficial; $x = 22$.

F. Order *Hymenophyllales*

6. Family *Hymenophyllaceae* (filmy ferns; incl. *Trichomanaceae*). Nine genera (Ebihara *et al.*, 2006), two major clades (Pryer *et al.*, 2001b), “trichomanoid” and “hymenophylloid,” roughly corresponding to the classical genera *Trichomanes s.l.* and *Hymenophyllum s.l.* Ca. 600 species; monophyletic (Hasebe *et al.*, 1996; Dubuisson, 1996, 1997; Pryer *et al.*, 2001b, 2004b; Ebihara *et al.*, 2002, 2006; Dubuisson *et al.*, 2003; Hennequin *et al.*, 2003). Several segregate and monotypic genera are nested within *Hymenophyllum s.l.*: *Cardiomanes*, *Hymenoglossum*, *Rosenstockia*, and *Serpillopsis* (Ebihara *et al.*, 2002, 2006; Hennequin *et al.*, 2003, 2006a, 2006b). Several other classically defined hymenophylloid genera (subgenera) are not monophyletic, e.g., *Mecodium* and *Sphaerocionium* (Hennequin *et al.*, 2003, 2006a, 2006b; Ebihara *et al.*, 2006). *Microtrichomanes* appears to be polyphyletic (Ebihara *et al.*, 2004). *Trichomanes s.l.* comprises eight monophyletic groups that are regarded here as genera: *Abrodictyum*, *Callistopteris*, *Cephalomanes*, *Crepidomanes*, *Didymoglossum*, *Polyphlebium*, *Trichomanes s.s.*, and *Vandenboschia*; several of these have been subdivided into putatively monophyletic subgenera and sections (Ebihara *et al.*, 2006). Terrestrial and epiphytic; pantropical and south-temperate, but gametophytes survive in north-temperate regions as far north as Alaska (Farrar, 1993, p. 191). Characters: rhizomes slender, creeping, wiry, or sometimes erect and stouter, protostelic; vernation circinate; blades one cell thick between veins (a few exceptions); stomata lacking; cuticles lacking or highly reduced; scales usually lacking on blades, indument sometimes of hairs; sori marginal, indusia conical (campanulate), tubular, or clam-shaped (bivalvate), with receptacles (at least in trichomanoid genera) usually elongate, protruding from the involucre; sporangia maturing gradately in basipetal fashion, each with an uninterrupted, oblique annulus; spores green, globose, trilete; gametophytes filamentous or ribbon-like, often reproducing by fragmentation or production of gemmae; $x = 11, 12, 18, 28, 32, 33, 34, 36$, and perhaps others.

G. Order *Gleicheniales*

(incl. *Dipteridales*, *Matoniales*, *Stromatopteridales*). Monophyletic (Pryer *et al.*, 2004b; Schuettpelz *et al.*, 2006). Characters: root steles with 3–5 protoxylem poles (Schneider, 1996a); antheridia with 6–12 narrow, twisted or curved cells in walls.

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7. Family Gleicheniaceae (gleichenioids, forking ferns; incl. Dicranopteridaceae, Stromatopteridaceae). Six genera (*Dicranopteris*, *Diplopterygium*, *Gleichenella*, *Gleichenia*, *Sticherus*, *Stromatopteris*), ca. 125 species; monophyletic (Hasebe *et al.*, 1996; Pryer *et al.*, 1996, 2001a, 2004b). HENNIPMAN (1996) also suggested inclusion of the next two families in Gleicheniaceae; however, we recognize these as distinct based on their significant morphological disparity. Fossil record beginning in Cretaceous (Jurassic and older fossils may belong to the Gleicheniales or represent ancestors of extant Gleicheniaceae); pantropical. Characters: rhizomes with a “vitalized” protostele, or rarely solenostele; leaves indeterminate, blades pseudodichotomously forked (except *Stromatopteris*); veins free; sori abaxial, not marginal, with 5–15 sporangia, each with a transverse-oblique annulus, exindusiate, round, with 128–800 spores; sporangia maturing simultaneously within sori; spores globose-tetrahedral or bilateral; gametophytes green, surficial, with club-shaped hairs; $x = 22, 34, 39, 43, 56$.

8. Family Dipteridaceae (incl. Cheiroleuriaceae). Two genera (*Cheiroleuria*, *Dipteris*) from India, southeast Asia, eastern and southern China, central and southern Japan, and Malesia, to Melanesia and western Polynesia (Samoa), ca. 11 species; monophyletic (Kato *et al.*, 2001; Pryer *et al.*, 2004b). Fossil record beginning in upper Triassic. Characters: stems long-creeping, solenostelic or protostelic, covered with bristles or articulate hairs; petioles with a single vascular bundle proximally and polystelic distally; blades (sterile ones, at least) cleft into two or often more subequal parts; veins highly reticulate, with included veinlets; sori exindusiate, discrete, compital (served by many veins), scattered over the surface, or leaves dimorphic and the fertile ones covered with sporangia; sporangia maturing simultaneously or maturation mixed, with a four-seriate stalk; annuli almost vertical or slightly oblique; spores ellipsoid and monolete, or tetrahedral and trilete, 64 or 128 per sporangium; gametophytes cordate-thalloid; $x = 33$. *Dipteris* differs from *Cheiroleuria* primarily in having bilateral, monolete spores (tetrahedral and trilete in *Cheiroleuria*) and monomorphic leaves with discrete sori (sporangia acrostichoid in *Cheiroleuria*).

9. Family Matoniaceae (matonioids). Two genera (*Matonia*, *Phanerosorus*), each with two species; monophyletic, sister to Dipteridaceae (Kato and Setoguchi, 1998; Pryer *et al.*, 2004b; Schuettpelz *et al.*, 2006). Malesia–Pacific Basin; fossil record beginning in mid-Mesozoic. Characters: stems solenostelic with at least two concentric vascular cylinders (polycyclic) and a central vascular bundle; blades flabellate (*Matonia*), unevenly dichotomously branched or with dichotomous pinnae; veins free or slightly anastomosing around sori; sori with peltate indusia; sporangia maturing simultaneously, with very short stalks and oblique annuli; spores

globose-tetrahedral, trilete; gametophytes green, thalloid, with ruffled margins; antheridia large, many-celled; $x = 26$ (*Matonia*), 25 (*Phanerosorus*).

H. Order *Schizaeales*

Monophyletic (Hasebe *et al.*, 1996; Pryer *et al.*, 2001a, 2004b; Skog *et al.*, 2002; Wikström *et al.*, 2002). The three constituent families are given recognition because of their numerous, we consider significant, morphological differences, differences embracing gametophytes, stelar anatomy, leaf morphology, soral types, spores, and chromosome numbers. Fossil record beginning in the Jurassic (Collinson, 1996). Characters: fertile–sterile leaf blade differentiation; absence of well-defined sori; sporangia each with a transverse, subapical, continuous annulus.

10. Family Lygodiaceae (climbing ferns). A single genus (*Lygodium*), ca. 25 species; monophyletic (Skog *et al.*, 2002; Wikström *et al.*, 2002). Terrestrial, pantropical. Characters: rhizomes creeping, slender, protostelic, bearing hairs; leaves indeterminate, climbing, alternately pinnate; primary blade divisions (pinnae) pseudodichotomously forking with a dormant bud in the axils; veins free or anastomosing; sori on lobes of the ultimate segments; sporangia abaxial, solitary, one per sorus, each sporangium covered by an antrorse indusium-like subtending flange; spores 128–256 per sporangium, tetrahedral and trilete; gametophytes green, cordate, surficial; $x = 29, 30$.

11. Family Anemiaceae (incl. Mohriaceae). One genus (*Anemia*, incl. *Mohria*), ca. 100+ species; monophyletic (Skog *et al.*, 2002; Wikström *et al.*, 2002). Terrestrial; primarily New World, but a few species in Africa, India, and islands in the Indian Ocean. Characters: rhizomes creeping to suberect, bearing hairs; leaves determinate, mostly hemidimorphic or dimorphic; veins free, dichotomous, occasionally casually anastomosing; sporangia usually on a basal pair (sometimes more than two pinnae, or all pinnae modified and fertile) of skeletonized, highly modified, often erect pinnae; spores 128–256 per sporangium, tetrahedral, with strongly parallel ridges (Tryon and Lugardon, 1991); gametophytes green, cordate, surficial; $x = 38$.

12. Family Schizaeaceae. Two genera (*Actinostachys*, *Schizaea*), ca. 30 species; monophyletic (Skog *et al.*, 2002; Wikström *et al.*, 2002). The Cretaceous *Schizaeopsis* is the oldest fossil assigned to this lineage (Wikström *et al.*, 2002). Terrestrial, pantropical. Characters: blades simple (linear) or fan-shaped, variously cleft and with dichotomous free veins; sporangia on marginal, elaminate, branched or unbranched projections at blade tips, not in discrete sori, exindusiate; spores

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bilateral, monolete, 128–256 per sporangium; gametophytes green and filamentous (*Schizaea*), or subterranean and non-green, tuberous (*Actinostachys*); a puzzling array of base chromosome numbers: $x = 77, 94, 103$.

I. *Order Salviniiales*

(water ferns, heterosporous ferns; incl. “Hydropteridales,” Marsileales, Pilulariales). Monophyletic (Hasebe *et al.*, 1996; Pryer, 1999; Pryer *et al.*, 2001a, 2004b). The fossil *Hydropteris pinnata* provides evidence linking the two families of this order (Rothwell and Stockey, 1994; Pryer, 1999), although hypotheses differ about the exact relationships of *Hydropteris* with extant genera. Characters: fertile–sterile leaf blade differentiation; veins anastomosing; aerenchyma tissue often present in roots, shoots, and petioles; annulus absent; plants heterosporous, spores with endosporous germination; monomegasporous; gametophytes reduced.

13. Family Marsileaceae (clover ferns) (incl. Pilulariaceae). Three genera (*Marsilea*, *Pilularia*, *Regnellidium*), ca. 75 species total; monophyletic (Hasebe *et al.*, 1996; Pryer, 1999; Nagalingum *et al.*, 2007). Hennipman (1996) included both Salviniaceae and Azollaceae within Marsileaceae, but the spores of Marsileaceae differ markedly from those of Salviniaceae and Azollaceae (Schneider and Pryer, 2002). Rooted aquatics, in ponds, shallow water, or vernal pools, with floating or emergent leaf blades; subcosmopolitan. Characters: stems usually long-creeping, slender, often bearing hairs; leaflets 4, 2 or 0 per leaf; veins dichotomously branched but often fusing toward their tips; sori borne in stalked bean-shaped sporocarps (Nagalingum *et al.*, 2006), these arising from the rhizomes or from the base of the petioles, one to many per plant; heterosporous, microspores globose, trilete, megaspores globose, each with an acrolamella positioned over the exine aperture (Schneider and Pryer, 2002); perine gelatinous; $x = 10$ (*Pilularia*), 20 (*Marsilea*).

14. Family Salviniaceae (floating ferns, mosquito ferns; incl. Azollaceae). Two genera (*Salvinia*, *Azolla*), ca. 16 species; monophyletic (Pryer *et al.*, 1996, 2004b; Reid *et al.*, 2006; Metzgar *et al.*, in press). Some authors separate the genera into two families (Schneller in Kubitzki, 1990), a perfectly acceptable alternative, given the significant differences between the two genera. Plants free-floating, subcosmopolitan; fossil record beginning in Cretaceous (Collinson, 1996). Characters: roots present (*Azolla*) or lacking (*Salvinia*); stems protostelic, dichotomously branched; leaves sessile, alternate, small (ca. 1–25 mm long), round to oblong, entire; veins free (*Azolla*) or anastomosing (*Salvinia*); spores of two kinds (plants heterosporous), large megaspores and small microspores, these

globose, trilete; spore germination endoscopic; $x = 9$ (*Salvinia*), the lowest base chromosome number known in ferns, 22 (*Azolla*).

J. *Order Cyatheaales*

(tree ferns; incl. Dicksoniales, Hymenophyllopsidales, Loxomatales, Metaxyaales, Plagiogyriales) (Hasebe *et al.*, 1996; Wolf *et al.*, 1999; Pryer *et al.*, 2004b, Korall *et al.*, 2006b). Existing molecular evidence indicates a close relationship among the included families. The order is without obvious defining morphological characters: some of the species have trunk-like stems but others have creeping rhizomes; some have only hairs on the stems and blades, others have scales; sori are abaxial or marginal, either indusiate or exindusiate; spores are globose or tetrahedral-globose, each with a trilete scar; gametophytes green, cordate.

15. Family Thyrsopteridaceae. One genus (*Thyrsopteris*) with a single species, *T. elegans*, endemic to the Juan Fernández Islands; clearly related to tree ferns, but of uncertain phylogenetic position within this group (Korall *et al.*, 2006b). Characters: rhizomes ascending to erect, solenostelic, bearing runners, clothed with stiff, pluricellular hairs; leaves large, 2–3.5 m long; blades 3–5-pinnate, partially dimorphic (sori often restricted to proximal segments); blade axes adaxially grooved; veins free; sori terminal on the veins, the outer and inner indusia fused to form asymmetric cup-like structures, each sorus with a columnar, clavate receptacle; sporangia with oblique annuli; spores globose-tetrahedral, with prominent angles; $x =$ ca. 78.

16. Family Loxomataceae (often spelled Loxsomataceae). Two genera (*Loxoma*, *Loxomopsis*), each with a single species; monophyletic (Lehnert *et al.*, 2001; Pryer *et al.*, 2001a, 2004b; Korall *et al.*, 2006b). South American Andes, southern Central America, and New Zealand. Characters: rhizomes long-creeping, solenostelic, bearing hairs with a circular, multicellular base; blades bipinnate or more divided; veins free, forked; indument of uniseriate (*Loxomopsis*) to pluriseriate (*Loxoma*) bristles; sori marginal, terminal on veins, each with an urceolate indusium and elongate, often exserted receptacle; sporangia on thick, short stalks, with a slightly oblique annulus; spores tetrahedral, trilete; gametophytes with scale-like hairs (occurring also in some Cyatheaaceae); $x = 46$ (*Loxomopsis*), 50 (*Loxoma*).

17. Family Culcitaceae. One genus (*Culcita*) with two species; monophyletic (Korall *et al.*, 2006b). Sister to Plagiogyriaceae, and not closely related to *Calochlaena*, with which *Culcita* has historically been associated. This separation is supported by

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anatomical characters (White and Turner, 1988; Schneider, 1996a). Terrestrial; Azores, Madeira, Tenerife, southwestern Europe, and the Neotropics. Characters: rhizomes creeping or ascending, solenostelic, bearing articulate hairs; petioles in cross-section each with gutter-shaped vascular bundles; blades large, 4–5-pinnate-pinnatifid, sparingly hairy; veins free, often forked; sori to 3 mm wide, terminal on veins, paraphysate; outer indusia scarcely differentiated from the laminar tissue, inner noticeably modified; spores tetrahedral-globose, trilete; $x = 66$.

18. Family Plagiogyriaceae. A single genus (*Plagiogyria*), with ca. 15 species (Zhang and Nooteboom, 1998); monophyletic (Korall *et al.*, 2006b). Characters: stems creeping to usually erect, lacking hairs or scales; leaves dimorphic; blades pectinate to 1-pinnate; veins simple to 1-forked, free, or in fertile blades somewhat anastomosing at their ends; young leaves densely covered with pluricellular, glandular, mucilage-secreting hairs; sori exindusiate; sporangia borne on distal parts of veins, seemingly acrostichoid; sporangial stalks 6-rowed; annuli slightly oblique, continuous; spores tetrahedral, trilete; gametophytes green, cordate; $x = 66$?

19. Family Cibotiaceae. One genus (*Cibotium*), ca. 11 species; monophyletic, with some affinity to Dicksoniaceae, as circumscribed here (Korall *et al.*, 2006b). Terrestrial, amphipacific (eastern Asia, Malesia, Hawaii, southern Mexico, and Central America). Characters: rhizomes massive, creeping to ascending or erect (to 6 m), solenostelic or dictyostelic, bearing soft yellowish hairs at apices and persistent petiolar bases; fronds monomorphic, mostly 2–4 m long; petioles hairy at bases, with three corrugated vascular bundles arranged in an omega-shape; blades large, bipinnate to bipinnate-pinnatifid or more divided; secondary and tertiary blade axes adaxially ridged; veins free, simple or forked to pinnate; stomata with three subsidiary cells; sori marginal at vein ends, indusia bivalvate, each with a strongly differentiated, non-green outer indusium and a similarly modified tongue-like inner indusium, paraphyses filiform; spores globose-tetrahedral, with prominent angles and a well-developed equatorial flange; antheridial walls 5-celled; $x = 68$.

The spores of Cibotiaceae are unlike those of all other families in Cyatheales (Gastony, 1982; Tryon and Lugardon, 1991), with a prominent equatorial flange, and with usually thick, bold, \pm parallel, sometimes anastomosing ridges on the distal face; these ridges are the result of a coarsely ridged exospore, which is overlain by a thin, sometimes granulate perispore. The spores of *Lophosoria* (Dicksoniaceae) also have a prominent equatorial flange but lack distal ridges (Tryon and Lugardon, 1991; Tryon and Tryon, 1982). As far as is known, the

chromosome base number of $x = 68$ for *Cibotium* is also unique in the tree fern clade. The Hawaiian species have been extensively studied by Palmer (1994).

20. Family Cyatheaceae (cyatheoids, scaly tree ferns; incl. Alsophilaceae, Hymenophyllopsiaceae). Ca. five genera: *Alsophila* (incl. *Nephelea*), *Cyathea* (incl. *Cnemidaria*, *Hemitelia*, *Trichipteris*), *Gymnosphaera*, *Hymenophyllopsis*, *Sphaeropteris* (incl. *Fourniera*). *Alsophila*, as often construed, may be paraphyletic (Korall *et al.*, 2007); 600+ species; monophyletic, together with Dicksoniaceae, Metaxyaceae, and Cibotiaceae constituting the “core tree ferns” (Korall *et al.*, 2006b). Several studies have addressed relationships within Cyatheaceae (Conant *et al.*, 1996a, 1996b; Hasebe *et al.*, 1996; Stein *et al.*, 1996; Lantz *et al.*, 1999; Conant and Stein, 2001; Korall *et al.*, 2007), and circumscriptions of genera have varied widely (compare, e.g., Tryon, 1970; Holttum and Edwards, 1983). Several studies show convincingly that *Cnemidaria* nests within *Cyathea* (Conant *et al.*, 1996a, 1996b; Conant and Stein, 2001; Korall *et al.*, 2006b, 2007), and this close relationship is supported by the existence of sterile hybrids (see, e.g., Conant, 1975). Hennisman (1996) included all other families here placed in Cyatheales (excepting Hymenophyllopsiaceae, unplaced in his “consensus” classification) in his Cyatheaceae. *Hymenophyllopsis* (ca. eight species) has thin leaves lacking stomates, and is confined to the sandstone tepuis of the Guayana Shield (eastern Venezuela, Guyana, northern Brazil). It has nearly always been regarded as an isolated genus in its own family, or order (e.g., by Copeland, 1947; Pichi Sermolli, 1977; Tryon and Tryon, 1982). In the analysis by Wolf *et al.* (1999), a close relationship of *Hymenophyllopsis* to Cyatheaceae was suggested, based on a small taxonomic sampling. A larger sampling by Korall *et al.* (2006b) indicates that *Hymenophyllopsis*, as well as *Cnemidaria* and *Trichipteris*, all nest within *Cyathea*, and together form a well-supported neotropical clade. The spores of *Hymenophyllopsis* are remarkably similar to those of some species of *Cyathea* (compare, e.g., Figs. 14.8–14.11 with 26.15–26.18 in Tryon and Tryon, 1982). Characters associating *Hymenophyllopsis* with Cyatheaceae include the presence of true scales on the rhizomes, petiole bases, and sometimes on the blades. Tree ferns are mostly arborescent (but many exceptions known), and pantropical; fossils beginning in Jurassic or early Cretaceous.

Characters: stems with polycyclic dictyosteles, apices (and usually petiole bases) covered with large scales, sometimes also with trichomidia (scurf = small scales) or hairs; leaves usually large (to 5 m); petioles with obvious, usually discontinuous pneumathodes in two lines; blades 1–3-pinnate (rarely simple); veins simple to forked, free, rarely anastomosing (mostly in some *Cyathea*); sori superficial (abaxial) or terminal on the veins and marginal or submarginal (*Hymenophyllopsis*), round, exindusiate, or indusia saucer-like, cup-like, or globose

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and completely surrounding sporangia, or bivalvate (*Hymenophyllopsis*); sporangia maturing gradately, with oblique annuli; receptacles raised; paraphyses usually present; spores tetrahedral, trilete, variously ornamented; gametophytes green, cordate; $x = 69$ (*Hymenophyllopsis* not yet counted).

21. Family Dicksoniaceae, *nom. cons.* (dicksonioids; incl. Lophosoriaceae). Three genera (*Calochlaena*, *Dicksonia*, *Lophosoria*). Ca. 30 species; monophyletic (Korall *et al.*, 2006b). Terrestrial; eastern Asia, Australasia, Neotropics, St. Helena. Characters: mostly arborescent or with erect or ascending rhizomes; rhizomes with polycyclic dictyosteles, or solenostelic (*Calochlaena*); stem apices and usually petiolar bases covered with uniseriate hairs; blades large, 2–3 pinnate; veins simple to forked, free; sori abaxial and exindusiate (*Lophosoria*) or marginal (*Calochlaena*, *Dicksonia*) and each with a bivalvate or cup-like indusium, the adaxial (outer) valve formed by the reflexed segment margin and often differently colored; sporangia with oblique annuli; receptacles raised; paraphyses often present, filiform; spores globose or tetrahedral, trilete; $x = 56$ (*Calochlaena*), 65 (*Dicksonia*, *Lophosoria*).

Lophosoria (three species) is distinctive in having spores with a prominent subequatorial flange, with the proximal face coarsely tuberculate, the distal face perforate. It has often been placed in its own family, Lophosoriaceae (Pichi Sermolli, 1977; Tryon and Tryon, 1982; Kramer in Kubitzki, 1990).

22. Family Metaxyaceae. A single genus (*Metaxya*), two species; monophyletic (Smith *et al.*, 2001). Terrestrial, Neotropics. Characters: rhizomes short-creeping to ascending, dorsiventral, solenostelic, apices covered with pluricellular hairs; petioles each with an omega-shaped, corrugated, vascular bundle; blades simply pinnate; veins free, simple or forked at the base, \pm parallel; sori abaxial, round, scattered in several ill-defined rows, often with several sori on the same vein, with numerous filiform paraphyses, exindusiate; sporangia maturing simultaneously; sporangial stalks 4-rowed; annuli vertical or slightly oblique; spores 64 per sporangium, globose, trilete; $x = 95, 96$.

K. *Order Polypodiales*

(incl. “Aspidiales,” Aspleniales, Athyriales, Blechnales, “Davalliales,” Dennstaedtiales, Dryopteridales, Lindsaeales, Lonchitidales, Monachosorales, Negripteridales, Parkeriales, Platyzomatales, Pteridales, Saccolomatales, Thelypteridales). Monophyletic (Hasebe *et al.*, 1996; Pryer *et al.*, 1996, 2001a, 2004b; Schneider *et al.* 2004d). Characters: indusia laterally or centrally attached (indusia lost in many lineages); sporangial stalks 1–3 cells thick, often long; sporangial maturation mixed; sporangia each with a vertical annulus interrupted by

the stalk and stomium; gametophytes green, usually cordate (sometimes ribbon-shaped in some epiphytes), surficial.

23. Family Lindsaeaceae (lindsaeoids; incl. Cystodiaceae, Lonchitidaceae). Ca. eight genera (*Cystodium*, *Lindsaea*, *Lonchitis*, *Odontosoria*, *Ormoloma*¹, *Sphenomeris*, *Tapeinidium*, *Xyopteris*¹); in an unpublished thesis, Barcelona (2000) advocated the establishment of three additional genera allied to *Odontosoria* and *Sphenomeris*. Ca. 200 species; most likely monophyletic (Wolf *et al.*, 1994; Pryer *et al.*, 2004b; Korall *et al.*, 2006a; Schuettpelz *et al.*, 2006). The inclusion of *Lonchitis* (traditionally associated with dennstaedtioid ferns) in Lindsaeaceae is puzzling on morphological grounds, but molecular evidence strongly suggests it belongs near the lindsaeoid ferns (Schuettpelz and Pryer, in press). Terrestrial, or infrequently epipetric or epiphytic, pantropical. Characters: roots with sclerenchymatous outer cortex combined with an innermost cortical layer six cells wide (Schneider, 1996a) (excepting *Lonchitis* and *Cystodium*); rhizomes short- to long-creeping, protostelic with internal phloem, or in a few taxa solenostelic, bearing generally narrow, basally attached, non-clathrate scales or uniseriate hairs; blades 1–3-pinnate or more divided, generally glabrous; veins usually free, forking, occasionally anastomosing, without included veinlets; sori marginal or submarginal, indusiate, indusia opening towards the margin (extrorse), sometimes also attached at the sides, or sori covered by the reflexed segment margin (*Lonchitis*); spores tetrahedral, trilete, infrequently bilateral, monolete; gametophytes green, cordate; $x = 34, 38, 39, 44, 47, 48, 49, 50, 51$, perhaps others.

The position of *Cystodium* is clearly among Polypodiales, and not Dicksoniaceae (Cyatheales), where it has historically been placed, e.g., by Kramer in Kubitzki (1990) and Stevenson and Loconte (1996). Croft (1986) discussed its differences from dicksonioids and elevated it to family rank. A relationship to other lindsaeoids is suggested by molecular evidence, and this is reflected in our classification. However, expanded taxon sampling within early-diverging lineages of Polypodiales is necessary to confirm this or to determine whether recognition of a monotypic family Cystodiaceae is warranted (Korall *et al.*, 2006a; Schuettpelz and Pryer, in press).

24. Family Saccolomataceae. One genus, ca. 12 species; apparently monophyletic, but more sampling is needed to determine whether the Old World species are congeneric with those from the New World. The relationships of *Saccoloma* (incl. *Orthiopteris*) have been contentious. Kramer (in Kubitzki, 1990) treated *Saccoloma* and Lindsaeoideae as subfamilies within Dennstaedtiaceae. Molecular data suggest that it lies at or near the base of the polypodialean radiation, just below *Cystodium* and *Lonchitis* (Schuettpelz and Pryer, in press). Terrestrial,

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pantropical. Characters: rhizomes short-creeping to erect and somewhat trunk-like (long-creeping in most Lindsaeaceae and Dennstaedtiaceae) and dictyostelic (usually solenostelic in Dennstaedtiaceae, protostelic with internal phloem in Lindsaeaceae); petioles each with an omega-shaped vascular strand (open end adaxial); blades pinnate to decompose, lacking articulate hairs (as found in Dennstaedtiaceae); veins free; sori terminal on the veins, indusia pouch- or cup-shaped; spores globose-tetrahedral, surface with distinctive \pm parallel, branched ridges; $x = \text{ca. } 63$.

25. Family Dennstaedtiaceae (dennstaedtioids; incl. Hypolepidaceae, Monachosoraceae, Pteridiaceae). Ca. 11 genera: *Blotiella*, *Coptodipteris*, *Dennstaedtia* (incl. *Costaricia*¹), *Histiopteris*, *Hypolepis*, *Leptolepia*, *Microlepia*, *Monachosorum*, *Oenotrichia* s.s.¹, *Paesia*, *Pteridium* (bracken). The north-temperate *Dennstaedtia punctilobula* (Michx.) T. Moore is aberrant in *Dennstaedtia*, probably rendering that genus polyphyletic (Schuettpelz and Pryer, in press). Ca. 170 species; monophyletic, if lindsaeoid ferns are excluded (Pryer *et al.*, 2004b; Schuettpelz *et al.*, 2006). Monachosoraceae nests within Dennstaedtiaceae (Wolf *et al.*, 1994; Wolf, 1996a, 1997; Pryer *et al.*, 2004b; Schuettpelz *et al.*, 2006). Terrestrial, sometimes scandent; pantropical. Characters: rhizomes mostly long-creeping, often siphonostelic or polystelic, bearing jointed hairs; petioles often with epipetiolar buds, usually with a gutter-shaped vascular strand (adaxial face open); blades often large, 2–3-pinnate or more divided; indument of hairs; veins free, forked or pinnate, rarely anastomosing and then without included veinlets; sori marginal or submarginal, linear or discrete, indusia linear or cup-like at blade margins, or reflexed over sori; spores tetrahedral and trilete, or reniform and monolete; gametophytes green, cordate; $x = 26, 29, 30, 31, 33, 34, 38, 46, 47, 48$, and probably others.

26. Family Pteridaceae. (pteroids or pteridoids); incl. Acrostichaceae, Actiniopteridaceae, Adiantaceae (adiantoids, maidenhairs), Antrophyaceae, Ceratopteridaceae, Cheilanthaceae (cheilanthoids), Cryptogrammeaceae, Hemionitidaceae, Negripteridaceae, Parkeriaceae, Platyzomataceae, Sinopteridaceae, Taenitidaceae (taenitidoids), Vittariaceae (vittarioids, shoestring ferns). Ca. 50 genera, 950 species; monophyletic (Prado *et al.*, 2007; Schuettpelz *et al.*, 2007). Constituent genera, some of them notoriously polyphyletic or paraphyletic and in need of redefinition (e.g., *Cheilanthes*), include *Acrostichum*, *Actiniopteris*, *Adiantopsis*, *Adiantum*, *Aleuritopteris*, *Ananthacorus*, *Anetium*, *Anogramma*, *Antrophyum*, *Argyrochosma*, *Aspidotis*, *Astrolepis*, *Austrogramme*, *Bommeria*, *Cassebeera*, *Ceratopteris*, *Cerosora*¹, *Cheilanthes*, *Cheiloplecton*, *Coniogramme*, *Cosentinia* (Nakazato and Gastony, 2001), *Cryptogramma*, *Doryopteris*, *Eriosorus*, *Haplopteris*, *Hecistopteris*, *Hemionitis*, *Holcochlaena*, *Jamesonia*, *Llavea*, *Mildella*, *Monogramma*, *Nephopteris*¹, *Neurocallis*

(probably nested within a portion of *Pteris* s.l.; Schuettpelz and Pryer, in press), *Notholaena*, *Ochropteris*, *Onychium*, *Paraceterach*, *Parahemionitis*, *Pellaea* (Kirkpatrick, in press), *Pentagramma*, *Pityrogramma*, *Platyloma*, *Platyzoma*, *Polytaenium*, *Pteris* (incl. *Afropteris*, *Anopteris*), *Pterozonium*, *Radiovittaria*, *Rheopteris*, *Scoliosorus*, *Syngramma*, *Taenitis*, *Trachypteris*, and *Vittaria*. The family thus defined is monophyletic (Gastony and Rollo, 1996, 1998; Hasebe *et al.*, 1996; Pryer *et al.*, 1996; Gastony and Johnson, 2001; Schneider *et al.* 2004c; Zhang *et al.*, 2005; Prado *et al.*, 2007). Pteridaceae comprises five monophyletic groups (Prado *et al.*, 2007; Schuettpelz and Pryer, in press; Schuettpelz *et al.*, 2007), and if it were to be formally subdivided to reflect this, at either family or subfamily rank, the following taxa could be recognized: (1) Parkeriaceae, or Parkerioideae (*Acrostichum* and *Ceratopteris*); (2) Adiantaceae, or Adiantoideae, but Vittarioideae and Antrophyoideae have priority at subfamily rank (*Adiantum* and the ten vittarioid genera; Crane *et al.*, 1996; Hasebe *et al.*, 1996; Hennipman, 1996; Crane, 1997; Huiet and Smith, unpublished data); (3) Cryptogrammaceae (comprising *Coniogramme*, *Cryptogramma*, and *Llavea*; Zhang *et al.*, 2005; Schuettpelz *et al.*, 2007), no subfamily name available; (4) Sinopteridaceae, or Cheilanthoideae, but Notholaenoideae has priority; and (5) Pteridaceae s.s., or Pteridoideae, containing *Pteris* (probably not monophyletic; Schuettpelz and Pryer, in press; Schuettpelz *et al.*, 2007), its immediate allies, and the taenitoid ferns (*Taenitis* and allies; Sánchez-Baracaldo, 2004a, 2004b).

Terrestrial, epipetric, or epiphytic, subcosmopolitan, but most numerous in tropics and arid regions. Characters: rhizomes long- to short-creeping, ascending, suberect, or erect, bearing scales (less often, only hairs); blades monomorphic, hemidimorphic, or dimorphic in a few genera, simple (mostly vittarioids), pinnate, or sometimes pedate, sometimes decompound; veins free and forking, or variously anastomosing and forming a reticulate pattern without included veinlets; sori marginal or intramarginal, lacking a true indusium, often protected by the reflexed segment margin, or sporangia along the veins; sporangia each with a vertical, interrupted annulus, receptacles not or only obscurely raised; spores globose or tetrahedral, trilete, variously ornamented; mostly $x = 29, 30$.

Platyzoma, sometimes recognized as an isolated monotypic family, is aberrant in having numerous tiny, pouchlike pinnae (100+ pairs per frond), distinctive finely ridged and reticulate spore ornamentation (Tryon and Lugardon, 1991), an unusual (in the family) chromosome base number ($x = 38$; Tindale and Roy, 2002), and dimorphic spores (so-called “incipient heterospory”; A. Tryon, 1964), but *Platyzoma* nests with other genera of Pteridaceae, subfamily Pteridoideae (Hasebe *et al.*, 1996; Pryer *et al.*, 1996), perhaps near the base of the subfamily (Hasebe *et al.*, 1996; Schuettpelz *et al.*, 2007).

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Ceratopteris (three species, monophyletic) nests within Pteridaceae in all molecular analyses, and it appears to be sister to *Acrostichum* (Hasebe *et al.*, 1996; Pryer *et al.*, 1996). It has a number of strong autapomorphies that separate it from other Pteridaceae: coarsely ridged spores with parallel striations; spores 32 or fewer per sporangium; sporangia with ill-defined annuli; aquatic habitat; $x = 38$. Consequently, many taxonomists have placed it in its own family, Parkeriaceae (e.g., Copeland, 1947; Pichi Sermolli, 1977). Many of these autapomorphies (reduced spore number, loss of annulus) are probably a consequence of the shift to aquatic habitats.

The vittarioid genera include: *Ananthacorus*, *Anetium*, *Antrophyum*, *Haplopteris*, *Hecistopteris*, *Monogramma*, *Polytaenium*, *Radiovittaria*, *Rheopteris*, *Scoliosorus*, and *Vittaria*. The presence of *Rheopteris* in this clade is now clear (Schuettpelz *et al.*, 2007; Huiet and Smith, unpublished data). Characters include linear, mostly simple blades, sori along veins or in linear grooves, clathrate stem scales; presence of “spicular” cells in blade epidermis (shared with a few genera of Pteridaceae, e.g., *Adiantum*). Spores in the vittarioid ferns are predominantly trilete, but reversals to the monolete condition have occurred in *Vittaria*.

27. Family Aspleniaceae (asplenioids, spleenworts). From one to ten genera (generic delimitation in doubt, in light of all recent molecular data, e.g., van den Heede *et al.*, 2003; Schneider *et al.*, 2004b, 2005; Perrie and Brownsey, 2005). Regardless of the classification adopted, a huge proportion of the species are in *Asplenium*, even if that genus is construed in a fairly strict sense; the segregate genera *Camptosorus*, *Loxoscaphe*, *Phyllitis*, and *Pleurosorus* clearly nest within *Asplenium s.l.*, or appear related to species heretofore generally placed in *Asplenium* (Murakami *et al.*, 1999; Gastony and Johnson, 2001; Schneider *et al.*, 2004b). So also are the generic segregates *Diellia* (endemic to Hawaii), *Pleurosorus*, *Phyllitis*, *Ceterach*, *Thamnopteris*, and several others little used in recent years (Murakami *et al.*, 1999; Pinter *et al.*, 2002; van den Heede *et al.*, 2003; Schneider *et al.*, 2005). One expects that the oft-recognized, but still unsampled, genera *Antigramma*¹, *Holodictyum*¹, *Schaffneria*¹, and *Sinephropteris*¹ also nest in *Asplenium*. *Hymenasplenium*, however, with a different chromosome base number than nearly all of the other segregates, as well as distinctive root characters (Schneider, 1996b; Schneider *et al.*, 2004b, 2005), appears to represent the sister clade to the rest of the species in the family, and this name could be adopted for a well-supported segregate genus. Ca. 700+ species; monophyletic (Murakami and Schaal, 1994; Hasebe *et al.*, 1996; Murakami *et al.*, 1999; Gastony and Johnson, 2001; van den Heede *et al.*, 2003; Perrie and Brownsey, 2005; Schneider *et al.*, 2005).

Terrestrial, epipetric, or epiphytic, subcosmopolitan, but most numerous in the tropics. Characters: rhizomes creeping, ascending, or suberect, bearing

clathrate scales at apices and petiole bases (and sometimes other axes); petioles with back-to-back C-shaped vascular strands, these fusing distally into an X-shape; blades monomorphic, usually lacking acicular hairs on axes and/or lamina, often with microscopic clavate hairs; veins pinnate or forking, usually free, infrequently reticulate and then without included veinlets; sori elongate (linear) along the veins, not usually back-to-back on the same vein, usually with laterally attached, linear indusia; sporangial stalks long, 1-rowed; spores reniform, monolete, with a decidedly winged perine; $x = 36$ (mostly), but $x = 38, 39$ in *Hymenasplenium* (Murakami, 1995), 38 in *Boniniella*.

28. Family Thelypteridaceae (thelypteroids or thelypteridoids; incl. "Sphaerostephanaceae"). Ca. 5–30 genera, depending on taxonomic viewpoint: commonly accepted segregates are *Cyclosorus* (incl. *Ampelopteris*¹, *Amphineuron*¹, *Chingia*, *Christella*, *Cyclogramma*¹, *Cyclosorus s.s.*, *Glaphyopteridopsis*, *Goniopteris*, *Meniscium*, *Mensorus*¹, *Mesophlebion*, *Pelazoneuron*, *Plesioneuron*, *Pneumatopteris*, *Pronephrium*, *Pseudocyclosorus*, *Sphaerostephanos*, *Stegnogramma*, *Steiropteris*, *Trigonospora*), *Macrothelypteris*, *Phegopteris*, *Pseudophegopteris*, and *Thelypteris* (incl. *Amauropelta*, *Coryphopteris*, *Metathelypteris*, *Oreopteris*, *Parathelypteris*, and *Thelypteris s.s.*) (see Holttum, 1971; Smith and Cranfill, 2002). Smith (in Kubitzki, 1990) advocated recognition of five genera. Existing studies suggest that the phegopteroid genera (*Macrothelypteris*, *Phegopteris*, *Pseudophegopteris*) constitute a monophyletic clade at the base of the family, sister to all other "genera" (Smith and Cranfill, 2002; Schuettpelz and Pryer, in press). These same studies also indicate the paraphyly or polyphyly of certain other segregates (e.g., *Christella*, *Pronephrium*), as well as the monophyly of other segregates (e.g., *Amauropelta*, *Goniopteris*; Schuettpelz and Pryer, in press). Clearly, much more sampling is needed to understand the complex relationships within this species-rich family. Ca. 950 species; monophyletic (Hasebe *et al.*, 1996; Smith and Cranfill, 2002; Yatabe *et al.*, 2002; Schuettpelz and Pryer, in press). Hennipman (1996) also included Blechnaceae and the athyroid ferns in this family, a definition that would make Thelypteridaceae difficult or impossible to define morphologically. It is unclear whether the numerous genera recognized by Holttum (1971 and later publications) will hold up when additional molecular sampling has been done.

Terrestrial, rarely epipetric, pantropical, a few temperate. Characters: rhizomes creeping, ascending, or erect, bearing scales at apices, these non-clathrate, usually bearing acicular hairs; petioles in cross-section with two elongate or crescent-shaped vascular bundles facing one another, these uniting distally into a gutter-shape; blades monomorphic or occasionally dimorphic, usually pinnate or pinnate-pinnatifid; veins pinnate, free to variously and usually very regularly

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anastomosing, with or without included veinlets; indument of acicular hyaline hairs on blades and rhizome scales; sori abaxial, round to oblong, rarely elongate along veins, with reniform indusia or exindusiate; sporangia with 3-rowed, short to long stalks; spores ellipsoid, monolete, perine winged to spinulose; $x = 27-36$. Indusia have been lost independently in many lineages within the family.

29. Family Woodsiaceae (athyrioids, lady ferns; incl. Athyriaceae, Cystopteridaceae). Ca. 15 genera as defined here, ca. 700 species, nearly 85% of them in the two main genera, *Athyrium* and *Diplazium* (incl. *Callipteris*, *Monomelangium*), which are both probably paraphyletic (Wang *et al.*, 2003). Other widely recognized genera include *Acystopteris*, *Cheilanthes*, *Cornopteris*, *Cystopteris*, *Deparia* (incl. *Lunathyrium*, *Dryothyrium*, *Athyriopsis*, and *Dictyodroma*; Sano *et al.*, 2000b), *Diplaziopsis*, *Gymnocarpium* (incl. *Currania*), *Hemidictyum*, *Homalosorus*, *Protowoodsia*¹, *Pseudocystopteris*, *Rhachidosorus*, and *Woodsia* (incl. *Hymenocystis*¹; see Shmakov, 2003). This family has been variously circumscribed, and its limits are still uncertain (Hasebe *et al.*, 1996; Sano *et al.*, 2000a, 2000b; Schuettpelz and Pryer, in press). Wang *et al.* (2004) divided Athyriaceae (excluding woodsoid ferns, in their circumscription), by far the largest component in our concept of Woodsiaceae, into five subfamilies: Cystopteroideae, Athyrioideae, Deparioideae, Diplazioideae, and Rhachidosoroideae. As delimited here, the Woodsiaceae *s.l.* may be paraphyletic with respect to the Aspleniaceae, Blechnaceae + Onocleaceae, and Thelypteridaceae clades, but support for this paraphyly, or alternatively for the monophyly of the family as here defined, is lacking in broad analyses (Hasebe *et al.*, 1996; Sano *et al.*, 2000a). Because of this uncertainty, combined with the morphological grounds for the recognition of the Woodsiaceae as here circumscribed, we believe it is premature to adopt the alternative of erecting (or resurrecting) numerous small families to house its constituent genera. The most aberrant genera, within the Woodsiaceae as circumscribed here, appear to be *Woodsia* itself, *Cystopteris*, *Gymnocarpium*, and *Hemidictyum* (Schuettpelz and Pryer, in press). Further sampling may support the recognition of several additional families.

Mostly terrestrial, subcosmopolitan. Characters: rhizomes creeping, ascending, or erect; scales at apices, these usually non-clathrate, glabrous, glandular, or ciliate; petioles with two elongate or crescent-shaped vascular bundles facing one another, these uniting distally into a gutter-shape; blades monomorphic, rarely dimorphic; veins pinnate or forking, free, uncommonly anastomosing and then without included veinlets; sori abaxial, round, J-shaped, or linear with reniform to linear indusia, or exindusiate; spores reniform, monolete, perine winged, ridged, or spiny; mostly $x = 40, 41$; also 31 (*Hemidictyum*), 33, 38, 39 (*Woodsia*), and 42 (*Cystopteris*).

30. Family Blechnaceae (blechnoids; incl. Stenochlaenaceae). Currently ca. nine genera recognized (*Blechnum s.l.*, *Brainea*, *Doodia*, *Pteridoblechnum*, *Sadleria*, *Salpichlaena*, *Steenisoblechnum*, *Stenochlaena*, *Woodwardia*). Most of the existing recognized genera nest within *Blechnum s.l.*, and their acceptance is dependent on a revised recircumscription of *Blechnum s.l.*, which is manifestly paraphyletic in its current usage (Nakahira, 2000; Cranfill, 2001; Shepherd *et al.*, 2007; Schuettpelz and Pryer, in press). Ca. 200 species; monophyletic, sister to Onocleaceae (Hasebe *et al.*, 1996; Cranfill, 2001; Cranfill and Kato, 2003). *Woodwardia* (incl. *Anchistea*, *Chieniopteris*, *Lorinseria*) appears to be an early-branching member of the Blechnaceae (Cranfill and Kato, 2003). Characters: rhizomes creeping, ascending, or erect, sometimes trunk-like, often bearing stolons, scaly at apex (and on blades), scales non-clathrate; petioles with numerous, round, vascular bundles arranged in a ring; leaves monomorphic or often dimorphic; veins pinnate or forking, free to variously anastomosing, areoles without included veinlets, on fertile leaves forming costular areoles bearing the sori; sori in chains or linear, often parallel and adjacent to midribs, indusiate, with linear indusia opening inwardly (toward midribs); sporangia with 3-rowed, short to long stalks; spores reniform, monolete, perine winged; gametophytes green, cordate; $x = 27, 28, 31-37$ (*Blechnum* and segregates, *Woodwardia*); 40 (*Salpichlaena*).

31. Family Onocleaceae (onocleoids). Four genera (*Matteuccia*, *Onoclea*, *Onocleopsis*, *Pentarhizidium*), five species; monophyletic, sister to Blechnaceae (Hasebe *et al.*, 1996; Gastony and Ungerer, 1997). Family circumscription follows Pichi Sermolli (1977) and Gastony and Ungerer (1997, their tribe Onocleaceae of Dryopteridaceae). Terrestrial, largely in north-temperate regions. Characters: rhizomes long- to short-creeping to ascending, sometimes stoloniferous (*Matteuccia* and *Onocleopsis*); leaves strongly dimorphic; petioles with two vascular bundles uniting distally into a gutter-shape; blades pinnatifid or pinnate-pinnatifid; veins free or anastomosing, lacking included veinlets; spores reniform, brownish to green; sori enclosed (sometimes tightly) by reflexed laminar margins, also with membranous, often fugacious true indusia; $x = 37$ (*Onoclea*), 39 (*Matteuccia*), 40 (*Onocleopsis*, *Pentarhizidium*).

32. Family Dryopteridaceae (dryopteroids or dryopteridoids; incl. "Aspidiaceae," Bolbitidaceae, Elaphoglossaceae, Hypodematiaceae, Peranemataceae). Ca. 30–35 genera, 1700 species, of which 70% are in four genera (*Ctenitis*, *Dryopteris*, *Elaphoglossum*, and *Polystichum*) (Li and Lu, 2006). Genera include *Acrophorus*, *Adenoderris*, *Arachniodes* (incl. *Lithostegia*, *Phanerophlebiopsis*; Li and Lu, 2006), *Ataxipteris*¹, *Bolbitis* (incl. *Egenolfia*), *Coveniella*¹, *Ctenitis*, *Cyclodium*, *Cyrtogonellum* (incl. *Cyrtomidictyum*), *Cyrtomium* (Lu *et al.*, 2005, 2007), *Didymochlaena*, *Dryopolystichum*¹, *Dryopsis*,

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Dryopteris (incl. *Acrorumohra*, *Nothoperanema*, and probably other segregates tentatively accepted in this paper; for *Nothoperanema*, see Geiger and Ranker, 2005; for *Acrorumohra*, see Li and Lu, 2006), *Elaphoglossum* (incl. *Microstaphyla*¹, *Peltapteris*; Rouhan *et al.*, 2004; Skog *et al.*, 2004), *Hypodematium*, *Lastreopsis*, *Leucostegia*, *Lomagramma*, *Maxonia*, *Megalastrum*, *Oenotrichia* p.p. (Tindale and Roy, 2002), *Olferisia*, *Peranema*, *Phanerophlebia*, *Polystichum* (incl. *Papuapteris*, *Plecosorus*, *Sorolepidium*; Little and Barrington, 2003; Driscoll and Barrington, 2007; Lu *et al.*, 2007), *Polybotrya*, *Polystichopsis*, *Revwattsia*¹ (Tindale and Roy, 2002), *Rumohra*, *Stenolepia*¹, *Stigmatopteris*, and *Teratophyllum*.

Terrestrial, epipetric, hemiepiphytic, or epiphytic, pantropical, also with many temperate representatives. Characters: rhizomes creeping, ascending, or erect, sometimes scandent or climbing, with non-clathrate scales at apices; petioles with numerous round, vascular bundles arranged in a ring; blades monomorphic, less often dimorphic, sometimes scaly or glandular, uncommonly hairy; veins pinnate or forking, free to variously anastomosing, with or without included veinlets; sori usually round, indusia round-reniform or peltate (lost in several lineages), or sori exindusiate, acrostichoid in a few lineages; sporangia with 3-rowed, short to long stalks; spores reniform, monolete, perine winged; $x = 41$ (nearly all genera counted), rarely 40 (presumably derived).

Dryopteridaceae, as defined here, is almost certainly monophyletic, if *Didymochlaena*, *Hypodematium*, and *Leucostegia* are excluded (Hasebe *et al.*, 1996; Tsutsumi and Kato, 2006; Schuettpelz and Pryer, in press). The inclusion of these three genera may render this family paraphyletic, but they are tentatively included here pending further studies to address their precise phylogenetic affinities. *Didymochlaena*, with a single species, has generally been associated with other members of the Dryopteridaceae (as here defined). The three closely related species of *Hypodematium*, on the other hand, have been variously treated: as composing a monogeneric family Hypodematiaceae; as allied to the athyroid ferns (e.g., by Kramer in Kubitzki, 1990, presumably based on the presence of two vascular bundles in the petiole bases); or close to *Dryopteris* (e.g., Tryon and Lugardon, 1991, using evidence from spore morphology). *Leucostegia* is nearly always placed in Davalliaceae (e.g., by Kramer, in Kubitzki, 1990), because of its similar indusia and sori terminal on the veins, but it differs from members of Davalliaceae in the terrestrial habit, the more strongly verrucate spores with rugulate perispore (Tryon and Lugardon, 1991), and $x = 41$ (versus $x = 40$ in Davalliaceae). In a molecular phylogenetic analysis by Schneider *et al.* (2004c), *Didymochlaena* and *Hypodematium* were resolved as sister to one another, and together sister to the remainder of the eupolypods I clade (their Figure 2), but support for these relationships was lacking. Tsutsumi and Kato (2006) found

support for a sister relationship between *Hypodematium* and *Leucostegia*, and also support for these as sister to the remaining eupolypods I, but *Didymochlaena* was unsampled in their analysis. In the analysis by Schuettpelz and Pryer (in press), these three genera form a weakly supported clade at the base of Dryopteridaceae. Based on these results, we therefore consider it premature to segregate these genera from the Dryopteridaceae.

The indusium, either reniform or peltate and superior in most members of Dryopteridaceae, has undergone remarkable transformation in some genera, e.g., *Peranema*, which has inferior, initially globose indusia, and *Acrophorus*, with shallow, \pm semicircular, cuplike indusia. The remarkably different indusia in *Peranema* are the basis for the segregate family Peranemataceae, recognized by some authorities, but it seems likely that this genus is very closely related to *Dryopteris*, and may not be separable even generically. Soral position in Dryopteridaceae is also remarkably variable, sori sometimes being borne on the tips of marginal teeth in *Dryopteris deparioides* (T. Moore) Kuntze subsp. *deparioides* (Fraser-Jenkins, 1989), or on elevated receptacles in *Stenolepia*. Indusia have been lost independently along many evolutionary lines in Dryopteridaceae, even within genera, e.g., in *Ctenitis*, *Dryopteris*, *Lastreopsis*, *Megalastrum*, *Phanerophlebia*, *Polystichum*, and *Stigmatopteris*, as well as in a suite of dimorphic genera, e.g., *Elaphoglossum*, *Maxonia*, *Olfersia*, and *Polybotrya*.

Within Dryopteridaceae, as defined here, nests *Elaphoglossum* (Hasebe *et al.*, 1996; Sano *et al.*, 2000a). Sometimes it is included in its own family Elaphoglossaceae (e.g., by Pichi Sermolli, 1977), with 600–800 species, many still undescribed. Elaphoglossaceae was regarded as comprising three genera by Pichi Sermolli (1977), but *Microstaphyla* and *Peltapteris* nest within *Elaphoglossum* (www.nybg.org/bsci/res/moran/elaphoglossum.html; Mickel and Atehortúa, 1980; Rouhan *et al.*, 2004; Skog *et al.*, 2004). Relationships of *Elaphoglossum* are often considered to be with *Lomariopsis* (Kramer in Kubitzki, 1990), but this is refuted by two unpublished topologies. Elaphoglossaceae, narrowly defined, is monophyletic (Skog *et al.*, 2004), but to exclude it from Dryopteridaceae *s.s.*, as delimited above, renders the latter paraphyletic. Characters of *Elaphoglossum* include simple blades (usually) and dimorphic leaves with acrostichoid sporangia.

Several authors have treated most of the genera within our concept of Dryopteridaceae, as well as Tectariaceae, Woodsiaceae, and Onocleaceae, as comprising a much larger family Dryopteridaceae *s.l.*, with slightly varying circumscriptions (e.g., Tryon and Tryon, 1982; Kramer in Kubitzki, 1990; Wagner and Smith, 1993). With such a broad circumscription, and unless several other well-circumscribed families (e.g., Aspleniaceae, Blechnaceae, Polypodiaceae, Thelypteridaceae) are included, Dryopteridaceae is certainly paraphyletic.

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33. Lomariopsidaceae (lomariopsids; incl. Nephrolepidaceae, sword ferns). Four genera (*Cyclopeltis*, *Lomariopsis*, *Nephrolepis*, *Thysanosoria*¹); ca. 70 species. Characters: rhizomes creeping or sometimes climbing (plants hemi-epiphytic); petioles with round vascular bundles arranged in a gutter-shape; blades 1-pinnate, pinnae entire or crenate, often articulate, auriculate in some genera; veins free, \pm parallel or pinnate; sori discrete, round, and with round-reniform to reniform indusia, or exindusiate, or sporangia acrostichoid and the fronds dimorphic; spores bilateral, monolete, variously winged or ornamented; $x = 41$ (lower numbers known in some *Lomariopsis* species).

Based on published and unpublished results (especially Schuettpelz and Pryer, in press), it appears likely that these genera form a monophyletic group, despite the fact that such an assemblage has never been proposed. Lomariopsidaceae (*sensu* Kramer in Kubitzki, 1990; Moran in Davidse *et al.*, 1995) was construed to comprise six genera (containing ca. 800+ species): *Bolbitis* (and segregates *Edanyoa*, *Egenolfia*), *Elaphoglossum*, *Lomagamma*, *Lomariopsis*, *Teratophyllum*, and *Thysanosoria*¹. We place all of the aforementioned genera except *Lomariopsis* (and *Thysanosoria*, which lacks molecular data, but appears to be closely related to *Lomariopsis*) in the Dryopteridaceae (see above). *Nephrolepis*, with ca. 20 species, has sometimes been included in a monogeneric family Nephrolepidaceae (Kramer in Kubitzki, 1990). There is support in some analyses for *Nephrolepis* as sister to a large clade comprising the Tectariaceae, Oleandraceae, Polypodiaceae, and Davalliaceae (Hasebe *et al.*, 1996; Schneider *et al.*, 2004c); however, *Lomariopsis* was not included in these analyses. When *Lomariopsis* is included, *Nephrolepis* is resolved as sister to it, and these two genera, in turn, are strongly supported as sister to the aforementioned larger clade (Tsutsumi and Kato, 2006) and therefore to be expunged from the Dryopteridaceae. Although we have here decided tentatively to include *Nephrolepis* in the Lomariopsidaceae, the monophyly of this clade requires additional scrutiny, and thus Nephrolepidaceae may eventually require recognition.

Lu and Li (2006a) attempted to show that *Cyclopeltis*, based on a sample from one species, and using only *rbcL* data, should be placed in Tectariaceae. However, their own molecular trees do not support this placement, and we also consider their sampling of genera to be inadequate for resolving affinities of this genus.

34. Family Tectariaceae (tectarioids; incl. "Dictyoxiphiaceae," "Hypoderraceae"). 8–15 genera: *Aenigmopteris*¹, *Arthropteris*, *Heterogonium*, *Hypoderris*¹, *Pleocnemia*, *Psammiosorus*, *Psomiocarpa*¹, *Pteridrys*, *Tectaria* s.l. (incl. *Amphiblestra*¹, *Camptodium*¹, *Chlamydogramme*¹, *Cionidium*, *Ctenitopsis*, *Dictyoxiphium*, *Fadyenia*, *Hemigramma*, *Pleuroderris*¹, *Pseudotectaria*¹, *Quercifilix*, and perhaps other genera mentioned above), and *Triplophyllum* (Holttum, 1986); ca. 230 species, most in *Tectaria* s.l.

Generic limits, especially within *Tectaria s.l.*, are still very much in doubt. With the definition given here, Tectariaceae appears monophyletic, with moderate support (Schuettpelz and Pryer, in press). Including Tectariaceae within an expanded Dryopteridaceae renders the latter polyphyletic. *Ctenitis*, *Lastreopsis*, and several other genera here included in Dryopteridaceae have often been considered closely related to tectarioid ferns (Pichi Sermolli, 1977; Holttum, 1986; Moran in Davidse *et al.*, 1995), but molecular data suggest otherwise (Hasebe *et al.*, 1996; Schuettpelz and Pryer, in press). Terrestrial, pantropical. Characters: rhizomes usually short-creeping to ascending, dictyostelic, bearing scales; petioles not abscising, with a ring of vascular bundles in cross-section; blades simple, pinnate, or bipinnate, sometimes decompose; indument of jointed, usually short stubby hairs on the axes, veins, and sometimes laminar tissue, especially on rachises and costae adaxially; veins free or often highly anastomosing, sometimes with included veinlets; indusia reniform or peltate (lost in several lineages); spores brownish, reniform, monolete, variously ornamented; $x = 40$ (a few genera with $x = 41$, some dyploids with $x = 39$).

Arthropteris is apparently not closely related to *Oleandra*, as previously suggested (Kramer in Kubitzki, 1990), nor to *Nephrolepis*, as suggested by Pichi Sermolli (1977). Analyses that have included it show it to be sister to tectarioid ferns (Hasebe *et al.*, 1996; Tsutsumi and Kato, 2006; Schuettpelz and Pryer, in press). *Psammiosorus*, a monotypic genus endemic to Madagascar, has in turn been placed close to *Arthropteris* (Kramer, in Kubitzki, 1990) or even within *Arthropteris* (Tryon and Lugardon, 1991, on the basis of spore ornamentation). Therefore, both *Arthropteris* and *Psammiosorus* are tentatively assigned to Tectariaceae, although a Tectariaceae that includes them is more difficult to define morphologically.

35. Oleandraceae. Monogeneric, ca. 40 species, sister to Davalliaceae + Polypodiaceae (Hasebe *et al.*, 1996; Schneider *et al.*, 2004c, 2004d; Tsutsumi and Kato, 2006). Kramer (in Kubitzki, 1990), included two genera in addition to *Oleandra*: *Arthropteris* (ca. 12 species), and *Psammiosorus* (monotypic), but with this broader circumscription, the family is clearly polyphyletic; we include both of these genera in Tectariaceae. Species are terrestrial, epilithic or often secondary hemiepiphytes. Characters: blades simple; leaves articulate, abscising cleanly upon senescence from pronounced phyllopodia; sori indusiate, indusia round-reniform; spores reniform, monolete; $x = 41$.

36. Family Davalliaceae (davallioids; excl. Gymnogrammitidaceae). Four or five genera: *Araiostegia*, *Davallia* (incl. *Humata*, *Parasorus*, *Scyphularia*), *Davallodes*, *Pachypleuria*; ca. 65 species. Monophyletic, sister to Polypodiaceae (Hasebe *et al.*, 1996; Ranker *et al.*, 2004; Schneider *et al.*, 2004c, 2004d; Tsutsumi and Kato, 2005),

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but more information needed. *Gymnogrammitis* and *Leucostegia* are often included in Davalliaceae but the former belongs in Polypodiaceae (Schneider *et al.*, 2002b), while the latter is seemingly allied to *Hypodematum* (Dryopteridaceae; Tsutsumi and Kato, 2005; Schuettpelz and Pryer, in press). Generic limits of *Araiostegia*, *Davallia*, and *Pachypleuria* relative to each other are ill defined, and all of these genera appear to be paraphyletic or polyphyletic (Tsutsumi and Kato, 2005). Paleotropics and subtropics, Pacific Basin. Characters: plants epiphytic (most genera) or epipetric; rhizomes long-creeping, dictyostelic, dorsiventral, bearing scales; old leaves cleanly abscising at petiole bases; blades usually 1–4-pinnate (rarely simple), monomorphic (rarely dimorphic); veins free, forking or pinnate; indument generally lacking on blades and axes, but sometimes of articulate hairs; sori abaxial, inframarginal to well back from the margin, \pm round, with cup-shaped to reniform or lunate indusia (rarely forming a submarginal coenosorus in *Parasorus*); sporangia with 3-rowed, usually long stalks; annuli vertical; spores ellipsoid, monolete, yellowish to tan, perine various, but usually not strongly winged or cristate; gametophytes green, cordate; $x = 40$.

37. Family Polypodiaceae (polygrams; incl. Drynariaceae, Grammitidaceae (grammitids), Gymnogrammitidaceae, Loxogrammaceae, Platyceriaceae, Pleurisoriopsidaceae). Ca. 56 genera, ca. 1200 species Pantropical, a few temperate. Genera include *Acrosorus*, *Adenophorus* (Ranker *et al.*, 2003), *Aglaomorpha* (incl. *Photinopteris*, *Merinthosorus*, *Pseudodrynaria*, *Holostachyum*; Janssen and Schneider, 2005), *Arthromeris*, *Belvisia*, *Calymmodon*, *Campyloneurum* (incl. *Hyalotrichopteris*; Kreier *et al.*, 2007), *Ceradenia*, *Christiopteris* (Kreier and Schneider, unpublished data), *Chrysogrammitis*, *Cochlidium*, *Colysis*, *Ctenopteris*, *Dicranoglossum*, *Dictymia*, *Drynaria* (Janssen and Schneider, 2005), *Enterosora*, *Goniophlebium* s.l., *Grammitis*, *Lecanopteris* (Haufler *et al.*, 2003), *Lellingeria*, *Lemmaphyllum*, *Lepisorus* (incl. *Platygyria*), *Leptochilus*, *Loxogramme* (including *Anarthropteris*, a monotype from New Zealand; Kreier and Schneider, 2006b), *Melpomene*, *Microgramma* (incl. *Solanopteris*), *Micropolypodium*, *Microsorium*, *Neochheiropteris* (incl. *Neolepisorus*), *Neurodium*, *Niphidium*, *Pecluma*, *Phlebodium*, *Phymatosorus*, *Platycerium* (Kreier and Schneider, 2006a), *Pleopeltis*, *Polypodiodes* (incl. *Metapolypodium*; Lu and Li, 2006b), *Polypodium*, *Prosaptia*, *Pyrrosia* (incl. *Drymoglossum*), *Scleroglossum*, *Selliguea* (incl. *Crypsinus*, *Polypodiopteris*), *Serpocaulon* (Smith *et al.*, 2006a), *Synammia* (Schneider *et al.*, 2006a), *Terpsichore*, *Themelium*, *Thylacopteris* (Schneider *et al.*, 2004a), and *Zygophlebia*¹. Additional monotypic genera, include *Caobangia*¹, *Drymotaenium*, *Gymnogrammitis* (Schneider *et al.*, 2002b), *Kontumia*¹ (Wu *et al.*, 2005), *Luisma*¹, *Pleurosoriopsis*, and *Podosorus*¹.

Polypodiaceae s.s., as often recognized (e.g., by Kramer in Kubitzki, 1990), is paraphyletic, because it excludes the grammitids, often segregated as Grammitidaceae (Ranker *et al.*, 2004; Schneider *et al.*, 2004d). Generic boundaries need

clarification, and, in particular, *Polypodium* and *Microsorium*, two of the largest assemblages, are known to be polyphyletic (Schneider *et al.*, 2004d; 2006b). Certain previously misplaced genera are now shown to be nested within Polypodiaceae, e.g., *Pleurosoriopsis* (Hasebe *et al.*, 1996, Schneider *et al.*, 2004d) and *Gymnogrammitis* (Schneider *et al.*, 2002b). Polypodiaceae contains large wholly Neotropical and wholly Paleotropical clades (Schneider *et al.*, 2004d; Haufler, 2007).

Mostly epiphytic and epipetric, a few terrestrial; pantropical. Characters: rhizomes long-creeping to short-creeping, dictyostelic, bearing scales; petioles cleanly abscising near their bases or not (most grammitids), leaving short phyllopodia; blades monomorphic or dimorphic, mostly simple to pinnatifid or 1-pinnate (uncommonly more divided); indument lacking or of hairs and/or scales on the blade; veins often anastomosing or reticulate, sometimes with included veinlets, or veins free (most grammitids); indument various, of scales, hairs, or glands; sori abaxial (rarely marginal), round to oblong or elliptic, occasionally elongate, or the sporangia acrostichoid, sometimes deeply embedded; sori exindusiate, sometimes covered by caducous scales when young (e.g., *Lepisorus*, *Pleopeltis*); sporangia with 1–3-rowed, usually long stalks, frequently with paraphyses on sporangia or on receptacle; spores hyaline to yellowish, reniform, and monolete (non-grammitids), or greenish and globose-tetrahedral, trilete (all grammitids); perine various, usually thin, not strongly winged or cristate; mostly $x = 35, 36, 37$ (25 and other numbers also known).

The grammitid ferns clearly nest within Polypodiaceae (Ranker *et al.*, 2004; Schneider *et al.*, 2004d). Tryon and Tryon (1982) and Hennipman (1996) have previously subsumed the grammitids in Polypodiaceae, as we now do here. Grammitids (ca. 20 genera, 600 species, pantropical) share a large number of morphological synapomorphies: veins free (mostly); scales lacking on blades; setiform, often dark red-brown hairs on leaves; sporangial stalks 1-rowed; spores green, trilete; gametophytes ribbon-shaped. Some genera of grammitids have been shown to be polyphyletic and their limits are the subject of re-interpretation, e.g., *Ctenopteris*, *Grammitis*, *Micropolypodium*, and *Terpsichore*, while others are likely monophyletic, e.g., *Ceradenia*, *Melpomene*, *Prosaptia* s.l. (Ranker *et al.*, 2004). Schuettpelz and Pryer (in press) support the newly described genus *Serpocaulon* (Smith *et al.*, 2006a) as sister to the grammitid ferns.

16.4 Synthesis: lessons learned from morphology and molecular systematics, and unexpected surprises

With the benefit of hindsight, it is instructive to note how classifications based on morphology have fared with the advent of molecular data. Further,

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we explore where more information is needed in order to better circumscribe natural lineages.

Many of the fern families recognized during the past one hundred years still have strong support, and clear evidence of monophyly, in the most recent large-scale molecular analysis (Schuettpelz and Pryer, in press). Bitypic or polytypic families (two or more genera) with essentially the same, or only minor, changes in circumscription from that utilized in most recent classifications include the eusporangiate families Marattiaceae, Ophioglossaceae, and Psilotaceae; early-diverging leptosporangiate families Cyatheaceae (with the addition of Hymenophyllopsidaceae), Dipteridaceae (including Cheiropleuriaceae), Gleicheniaceae (including Stromatopteris), Hymenophyllaceae, Loxomataceae, Marsileaceae, Matoniaceae, Osmundaceae, Salviniaceae *s.l.*, and Schizaeaceae *s.s.*; and more derived leptosporangiate families Aspleniaceae, Blechnaceae, and Thelypteridaceae (Table 16.1). Many monotypic families in older classifications are still recognized, e.g., Equisetaceae, Plagiogyriaceae, Metaxyaceae, and several new ones have been added by virtue of their seeming isolation (as judged from molecular and morphological analyses) from existing families: Thyrsopteridaceae, Culcitaceae, Cibotiaceae (all members of the order Cyatheales), and Saccolomataceae.

The biggest surprises have come from demonstration of relationships between taxa previously considered to be only remotely related. Among these, we mention: (1) the unanticipated sister relationship between Ophioglossaceae and Psilotaceae, which is shown by nearly all molecular analyses (e.g., Hasebe *et al.*, 1996; Manhart, 1996; Pryer *et al.*, 2001a, 2004b); (2) the intimate relationship of Equisetaceae with ferns, rather than with a grade of so-called fern allies (Pryer *et al.*, 2001a; but excluded from the ferns by Rothwell and Nixon, 2006, who include fossil data); and (3) the recognition of genera of previously uncertain placement (sometimes placed in monotypic families) in existing often diverse families, e.g., *Stromatopteris* (Stromatopteridaceae) in Gleicheniaceae (Pryer *et al.*, 2004b; Schuettpelz and Pryer, in press); *Cystodium* allied to lindsaeoid (rather than dicksonioid) ferns (Korall *et al.*, 2006a); *Hymenophyllopsis* in tree ferns (Wolf *et al.*, 1999), probably even nested in *Cyathea* itself (Korall *et al.*, 2006b); *Rheopteris* in Pteridaceae, among the vittarioid ferns (Schuettpelz *et al.*, 2007); *Leucostegia* among the dryopteroid ferns (rather than with Davalliaceae; Tsutsumi and Kato, 2006; Schuettpelz and Pryer, in press); *Gymnogrammitis* in Polypodiaceae (Schneider *et al.*, 2002b); and *Pleurosoriopsis* (Pleurosoriopsidaceae) in Polypodiaceae (Hasebe *et al.*, 1996; Schneider *et al.*, 2004d). Moreover, several relatively large, diverse families have been shown to nest within families considered distinct by many: Vittariaceae, Parkeriaceae, and Platyzomataceae within Pteridaceae

(Crane *et al.*, 1996; Gastony and Rollo, 1996, 1998; Hasebe *et al.*, 1996; Schuettpelz and Pryer, in press; Schuettpelz *et al.*, 2007); Grammitidaceae in Polypodiaceae (Schneider *et al.*, 2004d).

Other surprises have resulted from evidence that suggests that morphologically “odd,” small or monotypic genera nest within much larger, highly diverse genera, e.g., *Serpillopsis*, *Rosenstockia*, and *Hymenoglossum* within *Hymenophyllum* (Ebihara *et al.*, 2002, 2006; Hennequin *et al.*, 2003, 2006a, 2006b); *Diellia* within *Asplenium* (Schneider *et al.*, 2005). Other monotypic or small genera now recognized as probably better placed in larger genera include *Anarthropteris* (in *Loxogramme*, Polypodiaceae; Kreier and Schneider, 2006b); *Neurodium*, *Dicranoglossum*, and *Microphlebodium* (in *Pleopeltis*, Polypodiaceae; Schneider *et al.*, 2004d); *Ochropteris* and *Neurocallis* (in *Pteris*, Pteridaceae; Schuettpelz *et al.*, 2007); and almost all *Asplenium* segregates, e.g., *Camptosorus*, *Ceterach*, *Loxoscaphe*, *Phyllitis*, and *Pleurosorus* (in *Asplenium*, Aspleniaceae; Schneider *et al.*, 2004b). Unsampled monotypes likely to disappear once they can be scrutinized include *Schaffneria* and *Holodictyum* (in *Asplenium*); *Costaricia* (in *Dennstaedtia*); and *Amphiblestra*, *Cionidium*, *Fadyenia*, *Quercifilix*, and *Dictyoxiphium* (in *Tectaria*, Tectariaceae). However, a significant number of monotypic genera in a wide variety of families, are supported in molecular analyses, including *Stromatopteris* (Gleicheniaceae; Pryer *et al.*, 2004b, *Onoclea* (Onocleaceae; Gastony and Ungerer, 1997); *Regnellidium* (Marsileaceae; Pryer, 1999); *Helminthostachys* (Ophioglossaceae; Hasebe *et al.*, 1996); *Thylacopteris* (Polypodiaceae; Schneider *et al.*, 2004a); *Llavea* (Pteridaceae; Gastony and Rollo, 1998; Zhang *et al.*, 2005; Schuettpelz *et al.*, 2007); *Anetium* and *Ananthacorus* (Pteridaceae; Crane *et al.*, 1996; Crane, 1997).

Still other major generic-level recircumscriptions have been suggested or seem likely in Polypodiaceae, with a redefinition of *Polypodium*, *Pleopeltis*, and allied genera (Schneider *et al.*, 2004d; Smith *et al.*, 2006a), and in Pteridaceae, with a redefinition of *Pellaea* (Kirkpatrick, 2007).

It is now clear that many morphological characters traditionally utilized in fern classification, at family and higher ranks, are still extremely useful in characterizing monophyletic groups at these ranks. Among the more important and useful characters are, rhizome anatomy, venation pattern, indument type, indusial presence and type, spore type and ornamentation, eusporangiate versus leptosporangiate development, sporangial capacity, annulus position and form, chromosome base number, gametophyte morphology, and antheridial and archegonial characters. It is equally clear that certain characters usually given high importance in recognition of genera are highly homoplastic, and hence often of dubious importance, e.g., dimorphism and blade dissection.

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16.5 Future goals and directions

Although many questions have been satisfactorily resolved, at least in a preliminary way, other questions remain, with regard to relationships and circumscription of fern families and genera. At higher taxonomic levels, unresolved questions include: (1) circumscription of some families, in a monophyletic way, particularly Dryopteridaceae, Woodsiaceae, and Lomariopsidaceae *sensu* Smith *et al.* (2006b); (2) relationships of some genera and families, relative to other genera and families, e.g., *Saccoloma* (Saccolomataceae) and *Cystodium* (Lindsaeaceae?); and (3) circumscription of genera in some of the larger, more diverse families, particularly in Pteridaceae, Thelypteridaceae (Smith and Cranfill, 2002), Blechnaceae (Cranfill, 2001), Woodsiaceae, Dryopteridaceae, Davalliaceae (Tsutsumi and Kato, 2006), and Polypodiaceae (Ranker *et al.*, 2004; Schneider *et al.*, 2004d).

References

- Barcelona, J. F. (2000). Systematics of the fern genus *Odontosoria sensu lato* (Lindsaeaceae). Unpublished Ph.D. Thesis, Miami University, Oxford, OH.
- Bateman, R. M. (1991). Paleobiological and phylogenetic implications of anatomically-preserved *Archeocalamites* from the Dinantian of Oxroad Bay and Loch Humphrey Burn, southern Scotland. *Palaeontographica*, **B223**, 1–59.
- Bierhorst, D. W. (1971). *Morphology of Vascular Plants*. New York: Macmillan.
- Bower, F. O. (1926). *The Ferns (Filicales)*, Vol. 2, *The Eusporangiate and Other Relatively Primitive Ferns*. London: Cambridge University Press.
- Ching, R. C. (1940). On natural classification of the family “Polypodiaceae.” *Sunyatsenia*, **5**, 201–268.
- Ching, R. C. (1978). The Chinese fern families and genera: systematic arrangement and historical origin. *Acta Phytotaxonomica Sinica*, **16** (3), 1–19; **16** (4), 16–37.
- Christenhusz, M. J. M., Tuomisto, H., Metzgar, J., and Pryer, K. M. (in review). Evolutionary relationships within the neotropical, eusporangiate fern genus *Danaea* (Marattiaceae). *Molecular Phylogenetics and Evolution*.
- Christensen, C. (1938). Filicinae. In *Manual of Pteridology*, ed. F. Verdoorn. The Hague: Martinus Nijhoff, pp. 522–550.
- Collinson, M. E. (1996). “What use are fossil ferns?” – 20 years on: with a review of the fossil history of extant pteridophyte families and genera. In *Pteridology in Perspective*, ed. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens, pp. 349–394.
- Conant, D. S. (1975). Hybrids in American Cyatheaceae. *Rhodora*, **77**, 441–455.
- Conant, D. S. and Stein, D. B. (2001). Phylogenetic and geographic relationships of the tree ferns (Cyatheaceae) on Mount Kinabalu. *Sabah Parks Nature Journal*, **4**, 25–43.
- Conant, D. S., Raubeson, L. A., Attwood, D. K., Perera, S., Zimmer, E. A., Sweere, J. A., and Stein, D. B. (1996a). Phylogenetic and evolutionary implications of

- combined analysis of DNA and morphology in the Cyatheaceae. In *Pteridology in Perspective*, ed. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens, pp. 231–248.
- Conant, D. S., Raubeson, L. A., Attwood, D. K., and Stein, D. B. (1996b) [“1995”]. The relationships of Papuasian Cyatheaceae to New World tree ferns. *American Fern Journal*, **85**, 328–340.
- Copeland, E. B. (1947). *Genera Filicum*. Waltham, MA: Chronica Botanica.
- Crabbe, J. A., Jermy, A. C., and Mickel, J. T. (1975). A new generic sequence for the pteridophyte herbarium. *Fern Gazette*, **11**, 141–162.
- Crane, E. H. (1997). A revised circumscription of the genera of the fern family Vittariaceae. *Systematic Botany*, **22**, 509–517.
- Crane, E. H., Farrar, D. R., and Wendel, J. F. (1996) [“1995”]. Phylogeny of the Vittariaceae: convergent simplification leads to a polyphyletic *Vittaria*. *American Fern Journal*, **85**, 283–305.
- Cranfill, R. B. (2001). Phylogenetic studies in the Polypodiales (Pteridophyta) with an emphasis on the family Blechnaceae. Unpublished Ph.D. Thesis, University of California, Berkeley, CA.
- Cranfill, R. B. and Kato, M. (2003). Phylogenetics, biogeography and classification of the woodwardioid ferns (Blechnaceae). In *Pteridology in the New Millennium*, ed. S. Chandra and M. Srivastava. Dordrecht: Kluwer, pp. 25–48.
- Croft, J. R. (1986). The stipe and rachis vasculature of the dicksonioid fern, *Cystodium sorbifolium* (Cystodiaceae). *Kew Bulletin*, **41**, 789–803.
- Davidse, G., Sousa S., M., and Knapp, S. (eds.) (1995). *Flora Mesoamericana*, Vol. 1, *Psilotaceae a Salviniaceae*, ed. R. C. Moran and R. Riba. México: Universidad Nacional Autónoma de México.
- Davies, K. L. (1991). A brief comparative survey of aerophore structure within the Filicopsida. *Botanical Journal of the Linnean Society*, **197**, 115–137.
- Des Marais, D. L., Smith, A. R., Britton, D. M., and Pryer, K. M. (2003). Phylogenetic relationships and evolution of extant horsetails, *Equisetum*, based on chloroplast DNA sequence data (*rbcl* and *trnL-F*). *International Journal of Plant Sciences*, **164**, 737–751.
- Dickason, F. G. (1946). The ferns of Burma. *Ohio Journal of Science*, **46**, 109–141.
- Driscoll, H. E. and Barrington, D. S. (2007). Origin of Hawaiian *Polystichum* (Dryopteridaceae) in the context of a world phylogeny. *American Journal of Botany*, **94**, 1413–1424.
- Dubuisson, J.-Y. (1996). Evolutionary relationships within the genus *Trichomanes* sensu lato (Hymenophyllaceae) based on anatomical and morphological characters and a comparison with *rbcl* nucleotide sequences; preliminary results. In *Pteridology in Perspective*, ed. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens, pp. 285–287.
- Dubuisson, J.-Y. (1997). *rbcl* sequences: a promising tool for the molecular systematics of the fern genus *Trichomanes* (Hymenophyllaceae)? *Molecular Phylogenetics and Evolution*, **8**, 128–138.

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- Dubuisson, J.-Y., Hennequin, S., Douzery, E. J. P., Cranfill, R. B., Smith, A. R., and Pryer, K. M. (2003). *rbcl* phylogeny of the fern genus *Trichomanes* (Hymenophyllaceae), with special reference to neotropical taxa. *International Journal of Plant Sciences*, **164**, 753–761.
- Ebihara, A., Iwatsuki, K., Kurita, S., and Ito, M. (2002). Systematic position of *Hymenophyllum rolandi-principis* Rosenst. or a monotypic genus *Rosenstockia* Copel. (Hymenophyllaceae) endemic to New Caledonia. *Acta Phytotaxonomica et Geobotanica*, **53**, 35–49.
- Ebihara, A., Hennequin, S., Iwatsuki, K., Bostock, P. D., Matsumoto, S., Jaman, R., Dubuisson, J.-Y., and Ito, M. (2004). Polyphyletic origin of *Microtrichomanes* (Prantl) Copel. (Hymenophyllaceae), with a revision of the species. *Taxon*, **53**, 935–948.
- Ebihara, A., Dubuisson, J.-Y., Iwatsuki, K., Hennequin, S., and Ito, M. (2006). A taxonomic revision of Hymenophyllaceae. *Blumea*, **51**, 221–280.
- Farrar, D. R. (1993). Hymenophyllaceae. In *Flora of North America North of Mexico*, Vol. 2, ed. Flora of North America Editorial Committee. New York: Oxford University Press, pp. 190–197.
- Fraser-Jenkins, C. R. (1989). A monograph of *Dryopteris* (Pteridophyta: Dryopteridaceae) in the Indian subcontinent. *Bulletin of the British Museum (Natural History), Botany*, **18**, 323–477.
- Gastony, G. J. (1982). Spore morphology of the Dicksoniaceae. 2. The genus *Cibotium*. *Canadian Journal of Botany*, **60**, 955–972.
- Gastony, G. J. and Johnson, W. P. (2001). Phylogenetic placements of *Loxoscaphe thecifera* (Aspleniaceae) and *Actiniopteris radiata* (Pteridaceae) based on analysis of *rbcl* nucleotide sequences. *American Fern Journal*, **91**, 197–213.
- Gastony, G. J. and Rollo, D. R. (1996) [“1995”]. Phylogeny and generic circumscriptions of cheilanthoid ferns (Pteridaceae: Cheilantheoideae) inferred from *rbcl* nucleotide sequences. *American Fern Journal*, **85**, 341–360.
- Gastony, G. J. and Rollo, D. R. (1998). Cheilanthoid ferns (Pteridaceae: Cheilantheoideae) in the southwestern United States and adjacent Mexico – a molecular phylogenetic reassessment of generic lines. *Aliso*, **17**, 131–144.
- Gastony, G. J. and Ungerer, M. C. (1997). Molecular systematics and a revised taxonomy of the onocleoid ferns (Dryopteridaceae: Onocleaeae). *American Journal of Botany*, **84**, 840–849.
- Geiger, J. M. O. and Ranker, T. A. (2005). Molecular phylogenetics and historical biogeography of Hawaiian *Dryopteris* (Dryopteridaceae). *Molecular Phylogenetics and Evolution*, **34**, 392–407.
- Greuter, W., McNeill, J., Barrie, F. R., Burdet, H.-M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. C., Skog, J. E., Trehane, P., Turland, N. J., and Hawksworth, D. L. (eds.). (2000). *International Code of Botanical Nomenclature (Saint Louis Code)* [Regnum Vegetabile 138]. Königstein: Koeltz Scientific Books.
- Guillon, J. M. (2004). Phylogeny of horsetails (*Equisetum*) based on the chloroplast *rps4* gene and adjacent noncoding sequences. *Systematic Botany*, **29**, 251–259.
- Hasebe, M., Wolf, P. G., Pryer, K. M., Ueda, K., Ito, M., Sano, R., Gastony, G. J., Yokoyama, J., Manhart, J. R., Murakami, N., Crane, E. H., Haufler, C. H., and

- Hauk, W. D. (1996) ["1995"]. Fern phylogeny based on *rbcl* nucleotide sequences. *American Fern Journal*, **85**, 134–181.
- Haufler, C. H. (2007). Genetics, phylogenetics, and biogeography: considering how shifting paradigms and continents influence fern diversity. *Brittonia*, **59**, 108–114.
- Haufler, C. H., Grammer, W. A., Hennipman, E., Ranker, T. A., Smith, A. R., and Schneider, H. (2003). Systematics of the ant-fern genus *Lecanopteris* (Polypodiaceae): testing phylogenetic hypotheses with DNA sequences. *Systematic Botany*, **28**, 217–227.
- Hauk, W. D. (1996) ["1995"]. A molecular assessment of relationships among cryptic species of *Botrychium* subgenus *Botrychium* (Ophioglossaceae). *American Fern Journal*, **85**, 375–394.
- Hauk, W. D., Parks, C. R., and Chase, M. W. (2003). Phylogenetic studies of Ophioglossaceae: evidence from *rbcl* and *trnL-F* plastid DNA sequences and morphology. *Molecular Phylogenetics and Evolution*, **28**, 131–51.
- Hennequin, S., Ebihara, A., Ito, M., Iwatsuki, K., and Dubuisson, J.-Y. (2003). Molecular systematics of the fern genus *Hymenophyllum* s.l. (Hymenophyllaceae) based on chloroplastic coding and noncoding regions. *Molecular Phylogenetics and Evolution*, **27**, 283–301.
- Hennequin, S., Ebihara, A., Ito, M., Iwatsuki, K., and Dubuisson, J.-Y. (2006a). Phylogenetic systematics and evolution of the genus *Hymenophyllum* (Hymenophyllaceae: Pteridophyta). *Fern Gazette*, **17**, 247–257.
- Hennequin, S., Ebihara, A., Ito, M., Iwatsuki, K., and Dubuisson, J.-Y. (2006b). New insights into the phylogeny of the genus *Hymenophyllum* s.l. (Hymenophyllaceae): revealing the polyphyly of *Mecodium*. *Systematic Botany*, **31**, 271–284.
- Hennipman, E. (1996). Scientific consensus classification of Pteridophyta. In *Pteridology in Perspective*, ed. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens, pp. 191–202.
- Hill, C. R. and Camus, J. M. (1986). Evolutionary cladistics of marattialean ferns. *Bulletin of the British Museum (Natural History), Botany*, **14**, 219–300.
- Holttum, R. E. (1947). A revised classification of leptosporangiate ferns. *Journal of the Linnean Society, Botany*, **53**, 123–158.
- Holttum, R. E. (1949). The classification of ferns. *Biological Review*, **24**, 267–296.
- Holttum, R. E. (1971). Studies in the family Thelypteridaceae. III. A new system of genera in the Old World. *Blumea*, **19**, 17–52.
- Holttum, R. E. (1973). Posing the problems. In *The Phylogeny and Classification of the Ferns*, ed. A. C. Jermy, J. A. Crabbe, and B. A. Thomas, *Botanical Journal of the Linnean Society*, **67** (Suppl. 1), 1–10.
- Holttum, R. E. (1986). Studies in the genera allied to *Tectaria* Cav., V. *Triplophyllum*, a new genus of Africa and America. *Kew Bulletin*, **41**, 237–260.
- Holttum, R. E. and Edwards, P. (1983). The tree ferns of Mt. Roraima and neighboring areas of the Guayana Highlands with comments on the family Cyatheaceae. *Kew Bulletin*, **38**, 155–188.

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- Hoogland, R. D. and Reveal, J. L. (2005). Index nominum familiarum plantarum vascularium. *The Botanical Review*, **71**, 1–291.
- Janssen, T. and Schneider, H. (2005). Exploring the evolution of humus collecting leaves in drynarioid ferns (Polypodiaceae, Polypodiidae) based on phylogenetic evidence. *Plant Systematics and Evolution*, **252**, 175–197.
- Judd, W., Campbell, C. S., Kellogg, E. A., Stevens, P. F., and Donoghue, M. J. (2002). *Plant Systematics: A Phylogenetic Approach*, 2nd edn. Sunderland, MA: Sinauer.
- Kato, M. (1983). The classification of major groups of pteridophytes. *Journal of the Faculty of Science, University of Tokyo, Section III, Botany*, **13**, 263–283.
- Kato, M. (1987). A phylogenetic classification of Ophioglossaceae. *Gardens' Bulletin, Singapore*, **40**, 1–14.
- Kato, M. and Setoguchi, H. (1998). An *rbcL*-based phylogeny and heteroblastic leaf morphology of Matoniaceae. *Systematic Botany*, **23**, 391–400.
- Kato, M., Yatabe, Y., Sahashi, N., and Murakami, N. (2001). Taxonomic studies of *Cheiropleuria* (Dipteridaceae). *Blumea*, **46**, 513–525.
- Kenrick, P. and Crane, P. R. (1997). *The Origin and Early Diversification of Land Plants*. Washington, DC: Smithsonian Institution Press.
- Kirkpatrick, R. (2007). Investigating the monophyly of *Pellaea* (Pteridaceae) in the context of a phylogenetic analysis of cheilanthoid ferns. *Systematic Botany*, **32**, 504–518.
- Korall, P., Conant, D. S., Schneider, H., Ueda, K., Nishida, H., and Pryer, K. M. (2006a). On the phylogenetic position of *Cystodium*: it's not a tree fern – it's a polypod! *American Fern Journal*, **96**, 45–53.
- Korall, P., Pryer, K. M., Metzgar, J. S., Schneider, H., and Conant, D. S. (2006b). Tree ferns: monophyletic groups and their relationships as revealed by four protein-coding plastid loci. *Molecular Phylogenetics and Evolution*, **39**, 830–845.
- Korall, P., Conant, D. S., Metzgar, J. S., Schneider, H., and Pryer, K. M. (2007). A molecular phylogeny of scaly tree ferns (Cyatheaaceae). *American Journal of Botany*, **94**, 873–886.
- Kreier, H.-P. and Schneider, H. (2006a). Phylogeny and biogeography of the staghorn fern genus *Platynerium* (Polypodiaceae, Polypodiidae). *American Journal of Botany*, **93**, 217–225.
- Kreier, H.-P. and Schneider, H. (2006b). Reinstatement of *Loxogramme dictyopteris*, based on phylogenetic evidence, for the New Zealand endemic fern, *Anarthropteris lanceolata* (Polypodiaceae, Polypodiidae). *Australian Systematic Botany*, **19**, 309–314.
- Kreier, H.-P., Rojas-Alvarado, A. F., Smith, A. R., and Schneider, H. (2007). *Hyalotrichopteris* is indeed a *Campyloneurum* (Polypodiaceae). *American Fern Journal*, **97**, 127–135.
- Kubitzki, K. (ed.). (1990). *The Families and Genera of Vascular Plants*, Vol. 1, Pteridophytes and Gymnosperms, ed. K. U. Kramer and P. S. Green. Berlin: Springer-Verlag.
- Lantz, T. C., Rothwell, G. W., and Stockey, R. A. (1999). *Conantiopteris schuchmanii*, gen. et sp. nov., and the role of fossils in resolving the phylogeny of Cyatheaaceae s.l. *Journal of Plant Research*, **112**, 361–381.

- Lehnert, M., Mönnich, M., Pleines, T., Schmidt-Lebuhn, A., and Kessler, M. (2001). The relictual fern genus *Loxsomopsis*. *American Fern Journal*, **91**, 13–24.
- Li, C.-X. and Lu, C. G. (2006). Phylogenetic analysis of Dryopteridaceae based on chloroplast *rbcl* sequences. *Acta Phytotaxonomica Sinica*, **44**, 503–515.
- Little, D. P. and Barrington, D. S. (2003). Major evolutionary events in the origin and diversification of the fern genus *Polystichum* (Dryopteridaceae). *American Journal of Botany*, **90**, 508–514.
- Lovis, J. D. (1977). Evolutionary patterns and processes in ferns. In *Advances in Botanical Research*, Vol. 4, ed. R. D. Preston and H. W. Woolhouse. London: Academic Press, pp. 229–415.
- Lu, J.-M. and Li, D.-Z. (2006a). The study on systematic position of *Cyclopeltis*. *Acta Botanica Yunnanica*, **28**, 337–340.
- Lu, S.-G. and Li, C.-X. (2006b). Phylogenetic position of the monotypic genus *Metapolypodium* Ching endemic to Asia: evidence from chloroplast DNA sequences of *rbcl* gene and *rps4-trnS* region. *Acta Phytotaxonomica Sinica*, **44**, 494–502.
- Lu, J.-M., Li, D.-Z., Gao, L.-M., and Cheng, X. (2005). Paraphyly of *Cyrtomium* (Dryopteridaceae): evidence from *rbcl* and *trnL-F* sequence data. *Journal of Plant Research*, **118**, 129–135.
- Lu, J.-M., Barrington, D. S., and Li, D.-Z. (2007). Molecular phylogeny of the polystichoid ferns in Asia based on *rbcl* sequences. *Systematic Botany*, **32**, 26–33.
- Manhart, J. R. (1996) [“1995”]. Chloroplast 16S rDNA sequences and phylogenetic relationships of fern allies and ferns. *American Fern Journal*, **85**, 182–192.
- Metzgar, J. S., Schneider, H., and Pryer K., M. (in press). Phylogeny and divergence time estimates for the fern genus *Azolla* (Salviniaceae). *International Journal of Plant Sciences*.
- Mickel, J. T. (1974). Phyletic lines in the modern ferns. *Annals of the Missouri Botanical Garden*, **61**, 474–482.
- Mickel, J. T. and Atehortúa, L. G. (1980). Subdivision of the genus *Elaphoglossum*. *American Fern Journal*, **70**, 47–68.
- Miller, C. N., Jr. (1971). Evolution of the fern family Osmundaceae based on anatomical studies. *Contributions from the Museum of Paleontology, Ann Arbor, Michigan*, **23**, 105–169.
- Murakami, N. (1995). Systematics and evolutionary biology of the fern genus *Hymenasplenium* (Aspleniaceae). *Journal of Plant Research*, **108**, 257–268.
- Murakami, N. and Schaal, B. A. (1994). Chloroplast DNA variation and the phylogeny of *Asplenium* sect. *Hymenasplenium* (Aspleniaceae) in the New World tropics. *Journal of Plant Research*, **107**, 245–251.
- Murakami, N., Nogami, S., Watanabe, M., and Iwatsuki, K. (1999). Phylogeny of Aspleniaceae inferred from *rbcl* nucleotide sequences. *American Fern Journal*, **89**, 232–243.
- Murdock, A. (2005). Molecular evolution and phylogeny of marattioid ferns, an ancient lineage of land plants. www.2005.botanyconference.org/engine/search/index.php.

- Murdock, A. G., Reveal, J. L., and Doweld, A. (2006). (1746) Proposal to conserve the name Marattiaceae against Danaeaceae (Pteridophyta). *Taxon*, **55**, 1040–1042.
- Nagalingum, N. S., Schneider, H., and Pryer, K. M. (2006). Comparative morphology of reproductive structures in heterosporous water ferns and a re-evaluation of the sporocarp. *International Journal of Plant Sciences*, **167**, 805–815.
- Nagalingum, N. S., Schneider, H., and Pryer, K. M. (2007). Molecular phylogenetic relationships and morphological evolution in the heterosporous fern genus *Marsilea*. *Systematic Botany*, **32**, 16–25.
- Nakahira, Y. (2000). A molecular phylogenetic analysis of the family Blechnaceae, using the chloroplast gene *rbcl*. M. S. Thesis, Graduate School of Science, University of Tokyo, Tokyo.
- Nakazato, T. and Gastony, G. J. (2001). Molecular phylogenetics of *Anogramma* species and related genera (Pteridaceae: Taenitidoideae). In *Botany 2001, Plants and People*, Albuquerque, NM, Abstract.
- Nayar, B. K. (1970). A phylogenetic classification of the homosporous ferns. *Taxon*, **19**, 229–236.
- Palmer, D. D. (1994). The Hawaiian species of *Cibotium*. *American Fern Journal*, **84**, 73–85.
- Perrie, L. R. and Brownsey, P. J. (2005). Insights into the biogeography and polyploid evolution of New Zealand *Asplenium* from chloroplast DNA sequence data. *American Fern Journal*, **95**, 1–21.
- Pichi Sermolli, R. E. G. (1970). A provisional catalogue of the family names of living pteridophytes. *Webbia*, **25**, 219–297.
- Pichi Sermolli, R. E. G. (1973). Historical review of the higher classification of the Filicopsida. In *The Phylogeny and Classification of the Ferns*, ed. A. C. Jermy, J. A. Crabbe, and B. A. Thomas. *Botanical Journal of the Linnean Society*, **67** (Suppl. 1), 11–40.
- Pichi Sermolli, R. E. G. (1977). Tentamen pteridophytorum genera in taxonomicum ordinem redigendi. *Webbia*, **31**, 313–512.
- Pichi Sermolli, R. E. G. (1981). Report of the subcommittee for family names of Pteridophyta. *Taxon*, **30**, 163–168.
- Pichi Sermolli, R. E. G. (1982). A further contribution to the nomenclature of the families of Pteridophyta. *Webbia*, **35**, 223–237.
- Pichi Sermolli, R. E. G. (1986). Report of the subcommittee for family names of Pteridophyta. *Taxon*, **35**, 686–691.
- Pichi Sermolli, R. E. G. (1993). New studies on some family names of Pteridophyta. *Webbia*, **47**, 121–143.
- Pinter, I., Bakker, F., Barrett, J., Cox, C., Gibby, M., Henderson, S., Morgan-Richards, M., Rumsey, F., Russell, S., Trewick, S., Schneider, H., and Vogel, J. (2002). Phylogenetic and biosystematic relationships in four highly disjunct polyploid complexes in the subgenera *Ceterach* and *Phyllitis* in *Asplenium* (Aspleniaceae). *Organisms, Diversity, and Evolution*, **2**, 299–311.

- Prado, J., Rodrigues, C. D. N., Salatino, A., and Salatino, M. L. F. (2007). Phylogenetic relationships among Pteridaceae, including Brazilian species, inferred from *rbcl* sequences. *Taxon*, **56**, 355–368.
- Pryer, K. M. (1999). Phylogeny of marsileaceous ferns and relationships of the fossil *Hydropteris pinnata* reconsidered. *International Journal of Plant Sciences*, **160**, 931–954.
- Pryer, K. M., Smith, A. R., and Skog, J. E. (1996) [“1995”]. Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcl* sequences. *American Fern Journal*, **85**, 205–282.
- Pryer, K. M., Schneider, H., Smith, A. R., Cranfill, R., Wolf, P. G., Hunt, J. S., and Sipes, S. D. (2001a). Horsetails and ferns are a monophyletic group and the closest living relatives to seed plants. *Nature*, **409**, 618–622.
- Pryer, K. M., Smith, A. R., Hunt, J. S., and Dubuisson, J.-Y. (2001b). *rbcl* data reveal two monophyletic groups of filmy ferns (Filicopsida: Hymenophyllaceae). *American Journal of Botany*, **88**, 1118–1130.
- Pryer, K. M., Schneider, H., and Magallón, S. (2004a). The radiation of vascular plants. In *Assembling the Tree of Life*, ed. J. Cracraft and M. J. Donoghue. New York: Oxford University Press, pp. 138–153.
- Pryer, K. M., Schuettpelez, E., Wolf, P. G., Schneider, H., Smith, A. R., and Cranfill, R. (2004b). Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany*, **91**, 1582–1598.
- Qiu, Y.-L., et al. (2006). The deepest divergences in land plants inferred from phylogenomic evidence. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 15511–15516.
- Ranker, T. A., Geiger, J. M. O., Kennedy, S. C., Smith, A. R., Haufler, C. H., and Parris, B. S. (2003). Molecular phylogenetics and evolution of the endemic Hawaiian genus *Adenophorus* (Grammitidaceae). *Molecular Phylogenetics and Evolution*, **26**, 337–347.
- Ranker, T. A., Smith, A. R., Parris, B. S., Geiger, J. M. O., Haufler, C. H., Straub, S. C. K., and Schneider, H. (2004). Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy. *Taxon*, **53**, 415–428.
- Raubeson, L. A. and Jansen, R. K. (1992). Chloroplast DNA evidence on the ancient evolutionary split in vascular land plants. *Science*, **255**, 1697–1699.
- Reid, J. D., Plunkett, G. M., and Peters, G. A. (2006). Phylogenetic relationships in the heterosporous fern genus *Azolla* (Azollaceae) based on DNA sequence data from three noncoding regions. *International Journal of Plant Sciences*, **167**, 529–538.
- Renzaglia, K. S., Duff, R. J., Nickrent, D. L., and Garbary, D. J. (2000). Vegetative and reproductive innovations of early land plants; implications for a unified phylogeny. *Philosophical Transactions of the Royal Society of London, Series B*, **355**, 769–793.
- Rothwell, G. W. (1999). Fossils and ferns in the resolution of land plant phylogeny. *The Botanical Review*, **65**, 188–218.

- Rothwell, G. W. and Nixon, K. C. (2006). How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *International Journal of Plant Sciences*, **167**, 737–749.
- Rothwell, G. W. and Stockey, R. A. (1994). The role of *Hydropteris pinnata* gen. et sp. nov. in reconstructing the cladistics of heterosporous ferns. *American Journal of Botany*, **81**, 479–492.
- Rouhan, G., Dubuisson, J.-Y., Rakotondrainibe, F., Motley, T. J., Mickel, J. T., Labat, J.-N., and Moran, R. C. (2004). Molecular phylogeny of the fern genus *Elaphoglossum* (Elaphoglossaceae) based on chloroplast non-coding DNA sequences: contributions of species from the Indian Ocean area. *Molecular Phylogenetics and Evolution*, **33**, 745–763.
- Sánchez-Baracaldo, P. (2004a). Phylogenetics and biogeography of the neotropical fern genera *Jamesonia* and *Eriosorus* (Pteridaceae). *American Journal of Botany*, **91**, 274–284.
- Sánchez-Baracaldo, P. (2004b). Phylogenetic relationships of the subfamily Taenioideae, Pteridaceae. *American Fern Journal*, **94**, 126–142.
- Sano, R., Takamiya, M., Ito, M., Kurita, S., and Hasebe, M. (2000a). Phylogeny of the lady fern group, tribe Physematieae (Dryopteridaceae), based on chloroplast *rbcl* gene sequences. *Molecular Phylogenetics and Evolution*, **15**, 403–413.
- Sano, R., Takamiya, M., Kurita, S., Ito, M., and Hasebe, M. (2000b). *Diplazium subsinuatum* and *Di. tomitaroanum* should be moved to *Deparia* according to molecular, morphological, and cytological characters. *Journal of Plant Research*, **113**, 157–163.
- Schneider, H. (1996a.) Vergleichende Wurzelanatomie der Farne. Unpublished Ph.D. Thesis, Universität Zürich, Shaker, Aachen.
- Schneider, H. (1996b). Root anatomy of Aspleniaceae and the implications for systematics of the fern family. *Fern Gazette*, **12**, 160–168.
- Schneider, H. and Pryer, K. M. (2002). Structure and function of spores in the aquatic heterosporous fern family Marsileaceae. *International Journal of Plant Sciences*, **163**, 485–505.
- Schneider, H., Pryer, K. M., Cranfill, R., Smith, A. R., and Wolf, P. G. (2002a). Evolution of vascular plant body plans: a phylogenetic perspective. In *Developmental Genetics and Plant Evolution*, ed. Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins. London: Taylor and Francis, pp. 330–364.
- Schneider, H., Smith, A. R., Cranfill, R., Haufler, C. H., Ranker, T. A., and Hildebrand, T. (2002b). *Gymnogrammitis dareiformis* is a polygrammoid fern (Polypodiaceae) – resolving an apparent conflict between morphological and molecular data. *Plant Systematics and Evolution*, **234**, 121–136.
- Schneider, H., Janssen, T., Hovenkamp, P., Smith, A. R., Cranfill, R., Haufler, C. H., and Ranker, T. A. (2004a). Phylogenetic relationships of the enigmatic Malesian fern *Thylacopteris* (Polypodiaceae, Polypodiidae). *International Journal of Plant Sciences*, **165**, 1077–1087.
- Schneider, H., Russell, S. J., Cox, C. J., Bakker, F., Henderson, S., Gibby, M., and Vogel, J. C. (2004b). Chloroplast phylogeny of asplenoid ferns based on *rbcl* and *trnL-F*

- spacer sequences (Polypodiidae, Aspleniaceae) and its implications for the biogeography. *Systematic Botany*, **29**, 260–274.
- Schneider, H., Schuettpeiz, E., Pryer, K. M., Cranfill, R., Magallón, S., and Lupia, R. (2004c). Ferns diversified in the shadow of angiosperms. *Nature*, **428**, 553–557.
- Schneider, H., Smith, A. R., Cranfill, R., Hildebrand, T. E., Haufler, C. H., and Ranker, T. A. (2004d). Unraveling the phylogeny of polygrammoid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Molecular Phylogenetics and Evolution*, **31**, 1041–1063.
- Schneider, H., Ranker, T. A., Russell, S. J., Cranfill, R., Geiger, J. M. O., Agurauja, R., Wood, K. R., Grundmann, M., Kloberdanz, K., and Vogel, J. C. (2005). Origin of the endemic fern genus *Diellia* coincides with the renewal of Hawaiian terrestrial life in the Miocene. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, **272**, 455–460.
- Schneider, H., Kreier, H.-P., Wilson, R., and Smith, A. R. (2006a). The *Synammia* enigma: evidence for a temperate lineage of polygrammoid ferns (Polypodiaceae, Polypodiidae) in southern South America. *Systematic Botany*, **31**, 31–41.
- Schneider, H., Kreier, H.-P., Perrie, L. R., and Brownsey, P. J. (2006b). The relationships of *Microsorium* (Polypodiaceae) species occurring in New Zealand. *New Zealand Journal of Botany*, **44**, 121–127.
- Schuettpeiz, E. and Pryer, K. M. (in press). Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon*.
- Schuettpeiz, E., Korall, P., and Pryer, K. M. (2006). Plastid *atpA* data provide improved support for deep relationships among ferns. *Taxon*, **55**, 897–906.
- Schuettpeiz, E., Schneider, H., Huiet, L., Windham, M. D., and Pryer, K. M. (2007). A molecular phylogeny of the fern family Pteridaceae: assessing overall relationships and the affinities of previously unsampled genera. *Molecular Phylogenetics and Evolution*, **44**, 1172–1185.
- Scotland, R. W. and Wortley, A. H. (2003). How many species of seed plants are there? *Taxon* **52**, 101–104.
- Shepherd, L. D., Perrie, L. R., Parris, B. S., and Brownsey, P. J. (2007). A molecular phylogeny for the New Zealand Blechnaceae ferns from analysis of chloroplast *trnL-trnF* DNA sequences. *New Zealand Journal of Botany*, **45**, 67–80.
- Shmakov, A. I. (2003). Review of the family Woodsiaceae (Diels) Herter of Eurasia. In *Pteridology in the New Millennium*, ed. S. Chandra and M. Srivastava. Dordrecht: Kluwer, pp. 49–64.
- Skog, J. E., Mickel, J. T., Moran, R. C., Volovsek, M., and Zimmer, E. A. (2004). Molecular studies of representative species in the fern genus *Elaphoglossum* (Dryopteridaceae) based on cpDNA sequences *rbcl*, *trnL-F*, and *rps4-TRNS*. *International Journal of Plant Sciences*, **165**, 1063–1075.
- Skog, J. E., Zimmer, E., and Mickel, J. T. (2002). Additional support for two subgenera of *Anemia* (Schizaeaceae) from data for the chloroplast intergenic spacer region *trnL-F* and morphology. *American Fern Journal*, **92**, 119–130.
- Small, R. L., Lickey, E. B., Shaw, J., and Hauk, W. D. (2005). Amplification of noncoding chloroplast DNA for phylogenetic studies in lycophytes and

- monilophytes with a comparative example of relative phylogenetic utility from Ophioglossaceae. *Molecular Phylogenetics and Evolution*, **36**, 509–522.
- Smith, A. R. (1996) [“1995”]. Non-molecular phylogenetic hypotheses for ferns. *American Fern Journal*, **85**, 104–122.
- Smith, A. R. and Cranfill, R. B. (2002). Intrafamilial relationships of the thelypteroid ferns (Thelypteridaceae). *American Fern Journal*, **92**, 131–149.
- Smith, A. R., Tuomisto, H., Pryer, K. M., Hunt, J. S., and Wolf, P. G. (2001). *Metaxya lanosa*, a second species in the genus and fern family Metaxayaceae. *Systematic Botany*, **26**, 480–486.
- Smith, A. R., Kreier, H.-P., Haufler, C. H., Ranker, T. A., and Schneider, H. (2006a). *Serpocaulon* (Polypodiaceae), a new genus segregated from *Polypodium*. *Taxon*, **55**, 919–930.
- Smith, A. R., Pryer, K. M., Schuettpelz, E., Korall, P., Schneider, H., and Wolf, P. G. (2006b). A classification for extant ferns. *Taxon*, **55**, 705–731.
- Stein, D. B., Conant, D. S., and Valinski, A. E. C. (1996). The implications of chloroplast DNA restriction site variation on the classification and phylogeny of the Cyatheaceae. In *Holtum Memorial Volume*, ed. R. J. Johns. Kew: Royal Botanic Gardens, pp. 235–254.
- Stevenson, D. W. and Loconte, H. (1996). Ordinal and familial relationships of pteridophyte genera. In *Pteridology in Perspective*, ed. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens, pp. 435–467.
- Sun, B.-Y., Kim, M. H., Kim, C. H., and Park, C.-W. (2001). *Mankyua* (Ophioglossaceae): a new fern genus from Cheju Island, Korea. *Taxon*, **50**, 1019–1024.
- Tagawa, M. and Iwatsuki, K. (1972). Families and genera of the pteridophytes known from Thailand. *Memoirs of the Faculty of Science, Kyoto University, Series of Biology*, **5**, 67–88.
- Thorne, R. F. (2002). How many species of seed plants are there? *Taxon*, **51**, 511–522.
- Tindale, M. D. and Roy, S. K. (2002). A cytotoxic survey of the Pteridophyta of Australia. *Australian Systematic Botany*, **15**, 839–937.
- Tryon, R. M. (1952). A sketch of the history of fern classification. *Annals of the Missouri Botanical Garden*, **39**, 255–262.
- Tryon, A. F. (1964). *Platyzoma* – a Queensland fern with incipient heterospory. *American Journal of Botany*, **51**, 939–942.
- Tryon, R. (1970). The classification of the Cyatheaceae. *Contributions of the Gray Herbarium of Harvard University*, **200**, 1–53.
- Tryon, A. F. and Lugardon, B. (1991). *Spores of the Pteridophyta*. New York: Springer-Verlag.
- Tryon, R. M. and Tryon, A. F. (1982). *Ferns and Allied Plants, with Special Reference to Tropical America*. Berlin: Springer-Verlag.
- Tsutsumi, C. and Kato, M. (2005). Molecular phylogenetic study on Davalliaceae. *Fern Gazette*, **17**, 147–162.
- Tsutsumi, C. and Kato, M. (2006). Evolution of epiphytes in Davalliaceae and related ferns. *Botanical Journal of the Linnean Society*, **151**, 495–510.
- van den Heede, C. J., Viane, R. L. L., and Chase, M. W. (2003). Phylogenetic analysis of *Asplenium* subgenus *Ceterach* (Pteridophyta: Aspleniaceae) based on plastid and

- nuclear ribosomal ITS DNA sequences. *American Journal of Botany*, **90**, 481–493.
- Wagner, W. H., Jr. (1969). The construction of a classification. In *Systematic Biology*, United States National Academy of Sciences, Science Publication 1692. Washington, DC: National Academy Press, pp. 67–90.
- Wagner, W. H., Jr. and Smith, A. R. (1993). Pteridophytes of North America. In *Flora of North America North of Mexico*, Vol. 1, ed. Flora of North America Editorial Committee. New York: Oxford University Press, pp. 247–266.
- Wang, M.-L., Chen, Z.-D., Zhang, X.-C., Lu, S.-G., and Zhao, G.-F. (2003). Phylogeny of the Athyriaceae: evidence from chloroplast *trnL-F* region sequences. *Acta Phytotaxonomica Sinica*, **41**, 416–426.
- Wang, M.-L., Hsieh, Y.-T., and Zhao, G.-F. (2004). A revised subdivision of the Athyriaceae. *Acta Phytotaxonomica Sinica*, **42**, 524–527.
- White, R. A. and Turner, M. D. (1988). *Calochlaena*, a new genus of dicksonioid ferns. *American Fern Journal*, **78**, 86–95.
- Wikström, N. and Pryer, K. M. (2005). Incongruence between primary sequence data and the distribution of a mitochondrial *atp1* group II intron among ferns and horsetails. *Molecular Phylogenetics and Evolution*, **36**, 484–493.
- Wikström, N., Kenrick, P., and Vogel, J. C. (2002). Schizaeaceae: a phylogenetic approach. *Review of Palaeobotany and Palynology*, **119**, 35–50.
- Wolf, P. G. (1996a) [“1995”]. Phylogenetic analyses of *rbcl* and nuclear ribosomal RNA gene sequences in Dennstaedtiaceae. *American Fern Journal*, **85**, 306–327.
- Wolf, P. G. (1996b). Pteridophyte phylogenies based on analysis of DNA sequences: a multiple gene approach. In *Pteridology in Perspective*, ed. J. M. Camus, M. Gibby, and R. J. Johns. Kew: Royal Botanic Gardens, pp. 203–215.
- Wolf, P. G. (1997). Evaluation of *atpB* nucleotide sequences for phylogenetic studies of ferns and other pteridophytes. *American Journal of Botany*, **84**, 1429–1440.
- Wolf, P. G., Soltis, P. S., and Soltis, D. E. (1994). Phylogenetic relationships of dennstaedtioid ferns: evidence from *rbcl* sequences. *Molecular Phylogenetics and Evolution*, **3**, 383–392.
- Wolf, P. G., Pryer, K. M., Smith, A. R., and Hasebe, M. (1998). Phylogenetic studies of extant pteridophytes. In *Molecular Systematics of Plants II. DNA Sequencing*, ed. D. E. Soltis, P. S. Soltis, and J. J. Doyle. Boston, MA: Kluwer, pp. 541–556.
- Wolf, P. G., Sipes, S. D., White, M. R., Martines, M. L., Pryer, K. M., Smith, A. R., and Ueda, K. (1999). Phylogenetic relationships of the enigmatic fern families Hymenophyllopsidaceae and Lophosoriaceae: evidence from *rbcl* nucleotide sequences. *Plant Systematics and Evolution*, **219**, 263–270.
- Wu, S., Phan, K. L., and Xiang, J. (2005). A new genus and two new species of ferns from Vietnam. *Novon*, **15**, 245–249.
- Yatabe, Y., Nishida, H., and Murakami, N. (1999). Phylogeny of Osmundaceae inferred from *rbcl* nucleotide sequences and comparison to the fossil evidence. *Journal of Plant Research*, **112**, 397–404.
- Yatabe, Y., Watkins, J. E., Farrar, D. R., and Murakami, N. (2002). Genetic variation in populations of the morphologically and ecologically variable fern *Stegnogramma*

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pozo subsp. *mollissima* (Thelypteridaceae) in Japan. *Journal of Plant Research*, **115**, 29–38.

Yatabe, Y., Murakami, N., and Iwatsuki, K. (2005). *Claytosmunda*; a new subgenus of *Osmunda* (Osmundaceae). *Acta Phytotaxonomica et Geobotanica*, **56**, 127–128.

Zhang, X.-C. and Nooteboom, H. P. (1998). A taxonomic revision of Plagiogyriaceae (Pteridophyta). *Blumea*, **43**, 401–469.

Zhang, G., Zhang, X., and Chen, Z. (2005). Phylogeny of cryptogrammoid ferns and related taxa based on *rbcL* sequences. *Nordic Journal of Botany*, **23**, 485–493.

Appendix A: Familial names applied to extant ferns

Familial names applied to extant ferns, and their taxonomic disposition. Family names accepted by us are in **boldface**. Synonyms are in *italics*. Unpublished or otherwise illegitimate names are in quotation marks. An equal sign (=) is intended to indicate that we regard the first name as a heterotypic synonym of the family name we adopt.

Acrostichaceae Mett. ex A. B. Frank = Pteridaceae

Actiniopteridaceae Pic. Serm. = Pteridaceae

Adiantaceae Newman, *nom. cons.* over Parkeriaceae = Pteridaceae

Alsophilaceae C. Presl = Cyatheaceae

Anemiaceae Link; here included in Schizaeales

Angiopteridaceae Fée ex J. Bommer = Marattiaceae

Antrophyaceae Ching = Pteridaceae

“*Aspidiaceae*” Burnett, *nom. illeg.* = Dryopteridaceae

Aspleniaceae Newman; here included in Polypodiales

Athyriaceae Alston = Woodsiaceae

Azollaceae Wettst. = Salviniaceae

Blechnaceae Newman; here included in Polypodiales

Bolbitidaceae Ching = Dryopteridaceae

Botrychiaceae Horan. = Ophioglossaceae

Ceratopteridaceae Underw. = Parkeriaceae = Pteridaceae

Cheilanthaceae B. K. Nayar = Pteridaceae

Cheiropleuriaceae Nakai = Dipteridaceae

Christenseniaceae Ching = Marattiaceae

Cibotiaceae Korall; here included in Cyatheales

Cryptogrammaceae Pic. Serm. = Pteridaceae

Culcitaceae Pic. Serm.; here included in Cyatheales

Cyatheaceae Kaulf.; here included in Cyatheales

Cystodiaceae J. R. Croft = Lindsaeaceae

Cystopteridaceae Schmakov

Danaeaceae C. Agardh = Marattiaceae

Davalliaceae M. R. Schomb.; here included in Polypodiales

Dennstaedtiaceae Lotsy; here included in Polypodiales

Dicksoniaceae M. R. Schomb., *nom. cons.* over Thyrsopteridaceae; here included in Cyatheales

Dicranopteridaceae Ching ex Doweld = Gleicheniaceae
“*Dictyoxiphaceae*” Ching, *nom. nud.* = Tectariaceae
“*Didymochlaenaceae*” Ching, *nom. nud.* = Dryopteridaceae, tentatively
Dipteridaceae Seward and E. Dale; here included in Gleicheniales
Drynariaceae Ching = Polypodiaceae
Dryopteridaceae Herter, *nom. cons.* over *Peranemataceae*; here included in Polypodiales
Elaphoglossaceae Pic. Serm. = Dryopteridaceae
Equisetaceae Michx. ex DC.; here included in Equisetales
“*Filicaceae*” Juss., *nom. illeg.*
Gleicheniaceae C. Presl; here included in Gleicheniales
Grammitidaceae Newman [often misspelled *Grammitaceae*] = Polypodiaceae
Gymnogrammitidaceae Ching (incl. *Gymnogrammaceae*, spelling variant used by some authors) = Polypodiaceae
Helminthostachyaceae Ching = Ophioglossaceae
Hemionitidaceae Pic. Serm. = Pteridaceae
Hymenophyllaceae Mart.; here included in Hymenophyllales
Hymenophyllopsidaceae Pic. Serm. = Cyatheaceae
Hypodematiaceae Ching = Dryopteridaceae, tentatively
“*Hypoderrhiaceae*” Ching, *nom. nud.*, used by various authors, incl. Dickason (1946) = Tectariaceae
Hypolepidaceae Pic. Serm. = Dennstaedtiaceae
“*Kaulfussiaceae*” Campb., *nom. illeg.* = Marattiaceae
Lindsaeaceae C. Presl; here included in Polypodiales
Lomariopsidaceae Alston; here included in Polypodiales
Lonchitidaceae Doweld = Lindsaeaceae
Lophosoriaceae Pic. Serm.; here included in Dicksoniaceae
Loxogrammaceae Ching ex Pic. Serm. = Polypodiaceae
Loxomataceae C. Presl [often misspelled “*Loxsomaceae*”]; here included in Cyatheales
Lygodiaceae M. Roem.; here included in Schizaeales
Marattiaceae Kaulf., *nom. cons. prop.*; here included in Marattiales; antedated by Danaeaceae (Murdock *et al.*, 2006)
Marsileaceae Mirb.; here included in Salviniiales
Matoniaceae C. Presl; here included in Gleicheniales
Metaxyaceae Pic. Serm.; here included in Cyatheales
Mohriaceae C. F. Reed. = Anemiaceae
Monachosoraceae Ching = Dennstaedtiaceae
Negripteridaceae Pic. Serm. = Pteridaceae
Nephrolepidaceae Pic. Serm. = Lomariopsidaceae, tentatively
Oleandraceae Ching ex Pic. Serm.; here included in Polypodiales
Onocleaceae Pic. Serm.; here included in Polypodiales
Ophioglossaceae Martynov; here included in Ophioglossales
Osmundaceae Martynov; here included in Osmundales
Parkeriaceae Hook. = Pteridaceae
Peranemataceae (C. Presl) Ching = Dryopteridaceae

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Pilulariaceae Mirb. ex DC. (*Pilulariae*) = Marsileaceae
Plagiogyriaceae Bower; here included in Cyatheales
Platyneriaceae Ching = Polypodiaceae
Platydomataceae Nakai = Pteridaceae
Pleurosoriopsidaceae Kurita and Ikebe ex Ching = Polypodiaceae
Polypodiaceae J. Presl; here included in Polypodiales
Psilotaceae J. W. Griff. and Henfr.; here included in Psilotales
Pteridaceae E. D. M. Kirchn.; here included in Polypodiales
Pteridiaceae Ching = Dennstaedtiaceae
Saccolomataceae Doweld; here included in Polypodiales
Salviniaceae Martynov; here included in Salviniiales
Schizaeaceae Kaulf.; here included in Schizaeales
Sinopteridaceae Koidz., *nom. rej.* in favor of Adiantaceae = Pteridaceae
“*Sphaerostephanaceae*” Ching, *nom. nud.* = Thelypteridaceae
Stenochlaenaceae Ching = Blechnaceae
Stromatopteridaceae Bierh. = Gleicheniaceae
Taenitidaceae Pic. Serm. = Pteridaceae
Tectariaceae Panigrahi; here included in Polypodiales
Thelypteridaceae Pic. Serm.; here included in Polypodiales
Thyrsopteridaceae C. Presl; here included in Cyatheales
Tmesipteridaceae Nakai = Psilotaceae
Trichomanaceae Burmeist. = Hymenophyllaceae
Vittariaceae Ching = Pteridaceae
Woodsiaceae Herter; here included in Polypodiales

Appendix B: Index to genera

Index to genera with family assignments proposed in this classification. All accepted genera (but not all synonyms) in Kramer in Kubitzki (1990) are accounted for here. Genera newly described or recircumscribed since 1990 are also included. Accepted names are in roman, synonyms are in *italics*. Families are listed below with numbers in parentheses corresponding to the family numbers assigned in the text.

Ophioglossaceae (1)	Marsileaceae (13)
Psilotaceae (2)	Salviniaceae (14)
Equisetaceae (3)	Thyrsopteridaceae (15)
Marattiaceae (4)	Loxomataceae (16)
Osmundaceae (5)	Culcitaceae (17)
Hymenophyllaceae (6)	Plagiogyriaceae (18)
Gleicheniaceae (7)	Cibotiaceae (19)
Dipteridaceae (8)	Cyatheaceae (20)
Matoniaceae (9)	Dicksoniaceae (21)
Lygodiaceae (10)	Metaxyaceae (22)
Anemiaceae (11)	Lindsaeaceae (23)
Schizaeaceae (12)	Saccolomataceae (24)

Dennstaedtiaceae (25)
Pteridaceae (26)
Aspleniaceae (27)
Thelypteridaceae (28)
Woodsiaceae (29)
Blechnaceae (30)
Onocleaceae (31)

Dryopteridaceae (32)
Lomariopsidaceae (33)
Tectariaceae (34)
Oleandraceae (35)
Davalliaceae (36)
Polypodiaceae (37)

Abacopteris = *Cyclosorus*
Abrodictyum (6)
Acrophorus (32)
Acrorumohra = *Dryopteris*
Acrosorus (37)
Acrostichum (26)
Actiniopteris (26)
Actinostachys (12)
Acystopteris (29)
Adenoderris (32)
Adenophorus (37)
Adiantopsis (26)
Adiantum (26)
Aenigmopteris (34)
Afropteris = *Pteris*
Aglaomorpha (37)
Aleuritopteris (26)
Allantodia = *Diplazium*
Alsophila (20)
Amauropelta = *Thelypteris*
Ampelopteris = *Cyclosorus*
Amphiblestra = *Tectaria*
Amphineuron = *Cyclosorus*
Ananthacorus (26)
Anarthropteris = *Loxogramme*
Anchistea = *Woodwardia*
Anemia (11)
Anetium (26)
Angiopteris (4)
Anogramma (26)
Anopteris = *Pteris*
Antigramma = *Asplenium*
Antrophyum (26)
Arachniodes (32)
Araiostegia (36)
Archangiopteris = *Angiopteris*

Argyrochosma (26)
Arthromeris (37)
Arthropteris (34)
Aspidotis (26)
Aspleniopsis = *Austrogramme*
Asplenium (27)
Astrolepis (26)
Ataxipteris (32)
Athyriopsis = *Deparia*
Athyrium (29)
Austrogramme (26)
Azolla (14)
Belvisia (37)
Blechnum (30)
Blotiella (25)
Bolbitis (32)
Bommeria (26)
Botrychium (1)
Botrypus = *Botrychium*
Brainea (30)
Callipteris = *Diplazium*
Callistopteris (6)
Calochlaena (21)
Calymmodon (37)
Camptodium = *Tectaria*
Camptosorus = *Asplenium*
Campyloneurum (37)
Caobangia (37)
Cardiomanes = *Hymenophyllum*
Cassebeera (26)
Cephalomanes (6)
Ceradenia (37)
Ceratopteris (26)
Cerosora (26)
Ceterach = *Asplenium*
Ceterachopsis = *Asplenium*

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Cheilanthes (26)	Davallia (36)
Cheilanthopsis (29)	<i>Davalliopsis</i> = Trichomanes
Cheiloptecton (26)	Davallodes (36)
<i>Cheiroglossa</i> = Ophioglossum	Dennstaedtia (25)
Cheiropleuria (8)	Deparia (29)
<i>Chieniopteris</i> = Woodwardia	<i>Diacalpe</i> = Peranema
<i>Chingia</i> = Cyclosorus	Dicksonia (21)
<i>Chlamydogramme</i> = Tectaria	Dicranoglossum (37)
<i>Christella</i> = Cyclosorus	Dicranopteris (7)
Christensenia (4)	Dictymia (37)
Christiopteris (37)	<i>Dictyocline</i> = Cyclosorus
<i>Chrysochosma</i> = Notholaena	<i>Dictyodroma</i> = Deparia
Chrysogrammitis (37)	<i>Dictyoxiphium</i> = Tectaria
Cibotium (19)	Didymochlaena (32)
<i>Cionidium</i> = Tectaria	Didymoglossum (6)
<i>Cnemidaria</i> = Cyathea	<i>Diellia</i> = Asplenium
Cochlidium (37)	Diplaziopsis (29)
Colysis (37)	Diplazium (29)
Coniogramme (26)	Diplopterygium (7)
Coptodipteris (25)	Dipteris (8)
Cornopteris (29)	Doodia (30)
<i>Coryphopteris</i> = Thelypteris	Doryopteris (26)
Cosentinia (26)	<i>Drymoglossum</i> = Pyrrosia
<i>Costaricia</i> = Dennstaedtia	Drymotaenium (37)
Coveniella (32)	Drynaria (37)
Crepidomanes (6)	<i>Dryoathyrium</i> = Deparia
<i>Crypsinus</i> = Selliguela	Dryopolystichum (32)
Cryptogramma (26)	Dryopsis (32)
Ctenitis (32)	Dryopteris (32)
<i>Ctenitopsis</i> = Tectaria	<i>Edanyoa</i> = Bolbitis
Ctenopteris (37)	<i>Egenolfia</i> = Bolbitis
Culcita (17)	Elaphoglossum (32)
<i>Currania</i> = Gymnocarpium	Enterosora (37)
Cyathea (20)	Equisetum (3)
Cyclodium (32)	Eriosorus (26)
<i>Cyclogramma</i> = Cyclosorus	<i>Fadyenia</i> = Tectaria
Cyclopeltis (33)	<i>Feea</i> = Trichomanes
Cyclosorus (28)	<i>Fourniera</i> = Sphaeropteris
Cyrtogonellum (32)	<i>Glaphyroidopsis</i> = Cyclosorus
<i>Cyrtomidictyum</i> = Cyrtogonellum	<i>Glaphyopteris</i> = Cyclosorus
Cyrtomium (32)	Gleichenella (7)
Cystodium (23)	Gleichenia (7)
Cystopteris (29)	Goniophlebium (37)
Danaea (4)	<i>Goniopteris</i> = Cyclosorus

Gonocormus = *Crepidomanes*
Grammitis (37)
Gymnocarpium (29)
Gymnogramma = *Hemionitis*
Gymnopteris = *Hemionitis*
Gymnogrammitis (37)
Gymnosphaera = *Alsophila*
Haplopteris (26)
Hecistopteris (26)
Helminthostachys (1)
Hemidictyum (29)
Hemigramma = *Tectaria*
Hemionitis (26)
Hemitelia = *Cyathea*
Heterogonium (34)
Hippochaete = *Equisetum*
Histiopteris (25)
Holcochlaena (26)
Holodictyum = *Asplenium*
Holostachyum = *Aglaomorpha*
Homalosorus (29)
Humata = *Davallia*
Hyalotricha = *Campyloneurum*
Hyalotrichopteris = *Campyloneurum*
Hymenasplenium (27)
Hymenocystis = *Woodsia*
Hymenoglossum = *Hymenophyllum*
Hymenophyllopsis (20)
Hymenophyllum (6)
Hypodematium (32)
Hypoderris (34)
Hypolepis (25)
Idiopteris = *Pteris*
Jamesonia (26)
Japanobotrychium = *Botrychium*
Kontumia (37)
Kuniwatsukia = *Athyrium*
Lacostea = *Trichomanes*
Lacosteopsis = *Vandenboschia*
Lastrea = *Thelypteris*
Lastreopsis (32)
Lecanium = *Didymoglossum*
Lecanopteris (37)
Lellingeria (37)
Lemmaphyllum (37)
Lepisorus (37)
Leptochilus (37)
Leptogramma = *Cyclosorus*
Leptolepia (25)
Leptopteris (5)
Leptorumohra = *Arachniodes*
Leucostegia (32)
Lindsaea (23)
Lindsayoides = *Nephrolepis*
Lithostegia = *Arachniodes*
Litobrochia = *Pteris*
Llavea (26)
Lomagramma (32)
Lomaphlebia = *Grammitis?*
Lomaria = *Blechnum*
Lomariopsis (33)
Lonchitis (23)
Lophosoria (21)
Lorinseria = *Woodwardia*
Loxogramme (37)
Loxoma (16)
Loxoscaphe = *Asplenium*
Loxsomopsis (16)
Luisma (37)
Lunathyrium = *Deparia*
Lygodium (10)
Macroglena = *Abrodictyum*
Macrothelypteris (28)
Mankyua (1)
Marattia (4)
Marginariopsis = *Pleopeltis*
Marsilea (13)
Matonia (9)
Matteuccia (31)
Maxonia (32)
Mecodium = *Hymenophyllum*
Megalastrum (32)
Melpomene (37)
Meniscium = *Cyclosorus*
Menisorus = *Cyclosorus*
Merinthosorus = *Aglaomorpha*
Meryngium = *Hymenophyllum*
Mesophlebion = *Cyclosorus*

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<i>Metapolypodium</i> = Polypodiodes	<i>Papuapteris</i> = Polystichum
<i>Metathelypteris</i> = Thelypteris	Paraceterach (26)
Metaxya (22)	Parahemionitis (26)
<i>Microgonium</i> = Didymoglossum	<i>Parasorus</i> = Davallia
Microgramma (37)	<i>Parathelypteris</i> = Thelypteris
Microlepia (25)	Pecluma (37)
<i>Microphlebodium</i> = Pleopeltis	<i>Pelazoneuron</i> = Cyclosorus
Micropolypodium (37)	Pellaea (26)
Microsorium (37)	<i>Peltapteris</i> = Elaphoglossum
<i>Microstaphyla</i> = Elaphoglossum	Pentagramma (26)
<i>Microtrichomanes</i> = Hymenophyllum	Pentarhizidium (31)
Mildella (26)	Peranema (32)
<i>Mohria</i> = Anemia	Phanerophlebia (32)
Monachosorum (25)	Phanerosorus (9)
Monogramma (26)	Phegopteris (28)
<i>Monomelangium</i> = Diplazium	Phlebodium (37)
Neochheiropteris (37)	<i>Photinopteris</i> = Aglaomorpha
<i>Nephelea</i> = Alsophila	<i>Phyllitis</i> = Asplenium
Nephopteris (26)	Phymatosorus (37)
Nephrolepis (33)	Pilularia (13)
Neurocallis (26)	Pityrogramma (26)
Neurodium (37)	Plagiogyria (18)
<i>Neuromanes</i> = Trichomanes	Platycerium (37)
Niphidium (37)	<i>Platygyria</i> = Lepisorus
Notholaena (26)	Platyloma (26)
<i>Nothoperanema</i> = Dryopteris	Platzoma (26)
Ochropteris (26)	<i>Plecosorus</i> = Polystichum
Odontosoria (23)	Pleocnemia (34)
Oenotrichia (25)	Pleopeltis (37)
Oenotrichia p.p (32)	<i>Plesioneuron</i> = Cyclosorus
Oleandra (35)	<i>Pleuroderris</i> = Tectaria
Olfersia (32)	Pleurosoriopsis (37)
Onoclea (31)	<i>Pleurosorus</i> = Asplenium
Onocleopsis (31)	<i>Pneumatopteris</i> = Cyclosorus
Onychium (26)	Podosorus (37)
<i>Ophioderma</i> = Ophioglossum	Polybotrya (32)
Ophioglossum (1)	Polyphlebium (6)
<i>Oreopteris</i> = Thelypteris	Polypodiodes (37)
Ormoloma (23)	Polypodiopteris (37)
<i>Orthiopteris</i> = Saccoloma	Polypodium (37)
Osmunda (5)	Polystichopsis (32)
Osmundastrum (5)	Polystichum (32)
Pachypleuria (36)	Polytaenium (26)
Paesia (25)	<i>Pronephrium</i> = Cyclosorus
<i>Paltonium</i> = Neurodium	Prosaptia (37)

Protowoodsia (29)
Psammiosorus (34)
Pseudocolysis = *Pleopeltis*
Pseudocyclosorus = *Cyclosorus*
Pseudocystopteris (29)
Pseudodrynaria = *Aglaomorpha*
Pseudophegopteris (28)
Pseudotectaria = *Tectaria*
Psilotum (2)
Psomiocarpa (34)
Pteridium (25)
Pteridoblechnum (30)
Pteridrys (34)
Pteris (26)
Pterozonium (26)
Ptilopteris = *Monachorosum*
Pycnodoria = *Pteris*
Pyrrosia (37)
Quercifilix = *Tectaria*
Radiovittaria (26)
Regnellidium (13)
Revwattsia (32)
Rhachidosorus (29)
Rheopteris (26)
Rosenstockia = *Hymenophyllum*
Rumohra (32)
Saccoloma (24)
Sadleria (30)
Saffordia = *Trachypteris*
Sagenia = *Tectaria*
Salpichlaena (30)
Salvinia (14)
Sceptridium = *Botrychium*
Schaffneria = *Asplenium*
Schizaea (12)
Scleroglossum (26)
Scoliosorus (26)
Scyphularia = *Davallia*
Selliguea (37)
Serpocaulon (37)
Serpyllopsis = *Hymenophyllum*
Sinephropteris = *Asplenium*
Sinopteris = *Aleuritopteris*
Solanopteris = *Microgramma*
Sorolepidium = *Polystichum*
Sphaerocionium = *Hymenophyllum*
Sphaeropteris (20)
Sphaerostephanos = *Cyclosorus*
Sphenomeris (23)
Steenisiolechnum (30)
Stegnogramma = *Cyclosorus*
Steiropteris = *Cyclosorus*
Stenochlaena (30)
Stenolepia (32)
Sticherus (7)
Stigmatopteris (32)
Stromatopteris (7)
Synammia (37)
Syngamma (26)
Taenitis (26)
Tapeinidium (23)
Tectaria (34)
Teratophyllum (32)
Terpsichore (37)
Thamnopteris = *Asplenium*
Thelypteris (28)
Themelium (37)
Thylacopteris (37)
Thyrsopteris (15)
Thysanosoria (33)
Tmesipteris (2)
Todea (5)
Trachypteris (26)
Trichoneuron (32)
Trichipteris = *Cyathea*
Trichomanes (6)
Trigonospora = *Cyclosorus*
Triplophyllum (34)
Trismeria = *Pityrogramma*
Vaginularia = *Monogramma*
Vandenboschia (6)
Vittaria (26)
Weatherbya = *Lemmaphyllum*
Woodsia (29)
Woodwardia (30)
Xiphopteris = *Cochlidium*
Xyopteris (23)
Zygophlebia (37)