A classification for extant ferns

Alan R. Smith¹, Kathleen M. Pryer², Eric Schuettpelz², Petra Korall²,³, Harald Schneider⁴ & Paul G. Wolf⁵

¹ University Herbarium, 1001 Valley Life Sciences Building #2465, University of California, Berkeley, California 94720-2465, U.S.A. arsmith@berkeley.edu (author for correspondence).
² Department of Biology, Duke University, Durham, North Carolina 27708-0338, U.S.A.
³ Department of Phanerogamic Botany, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden.
⁴ Albrecht-von-Haller-Institut für Pflanzenwissenschaften, Abteilung Systematische Botanik, Georg-August-Universität, Untere Karspüle 2, 37073 Göttingen, Germany.
⁵ Department of Biology, Utah State University, Logan, Utah 84322-5305, U.S.A.

We present a revised classification for extant ferns, with emphasis on ordinal and familial ranks, and a synopsis of included genera. Our classification reflects recently published phylogenetic hypotheses based on both morphological and molecular data. Within our new classification, we recognize four monophyletic classes, 11 monophyletic orders, and 37 families, 32 of which are strongly supported as monophyletic. One new family, Cibotiaceae Korall, is described. The phylogenetic affinities of a few genera in the order Polypodiales are unclear and their familial placements are therefore tentative. Alphabetical lists of accepted genera (including common synonyms), families, orders, and taxa of higher rank are provided.

KEYWORDS: classification, Cibotiaceae, ferns, monilophytes, monophyletic.

Recent phylogenetic studies have revealed a basal dichotomy within vascular plants, separating the lycophytes (less than 1% of extant vascular plants) from the euphyllophytes (Fig. 1; Raubeson & Jansen, 1992; Kenrick & Crane, 1997; Pryer & al., 2001a, 2004a, b). Living euphyllophytes, in turn, comprise two major clades: the spermatophytes (seed plants), which are in excess of 260,000 species (Thorne, 2002; Scotland & Wortley, 2003), and the monilophytes (ferns, sensu Pryer & al., 2004b), with about 9,000 species, including horsetails, whisk ferns, and all euphorangiatae and leptosporangiatae ferns. Plants that are included 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. The focus of this reclassification is exclusively on ferns (Division Tracheophyta, Subdivision Euphyllophyta, Infradivision Moniliformoses, of Kenrick & Crane, 1997), characterized by lateral root origin in the endodermis, usually mesarch protoxylem in shoots, a pseudoendospore, plasmodial tapeum, and sperm cells with 30–1000 flagellae (Renzaglia & al., 2000; Schneider & al., 2002a).

Increasingly robust phylogenetic hypotheses for ferns (Hasebe & al., 1994, 1995; Manhart, 1994, 1995; Pryer & al., 1995, 2001a, 2004b; Kranz & Huss, 1996; Pahnke & al., 1996; Wolf, 1997; Wolf & al., 1998; Beckert & al., 1999; Vangerow & al., 1999; Sano & al., 2000a; Schneider & al., 2004c; Wikström & Pryer, 2005; Tsutsumi & Kato, 2006; Schuettpelz & al., in press), uti-
lizing data from morphology, seven chloroplast markers \((rbcL, \text{atpA}, \text{atpB}, \text{accD}, \text{rps}4, 16S \text{rDNA}, \text{ITS})\), one nuclear gene \((18\text{S rDNA})\), and three mitochondrial genes \((\text{atp}1, \text{nad}2, \text{nad}5)\) prompt us to reevaluate the classification of these vascular plants. Multiple-genre phylogenetic analyses, e.g., studies by Wolf (1996), Wolf & al. (1998), Przy & al. (2001a, 2004b), Schneider & al. (2004c), Wikström & Przy (2005), and Schuettpelz & al. (in press), have given rise to growing conviction in both the composition and relationships of taxa at familial and ordinal ranks. Five recent morphological analyses of relationships, by Przy & al. (1995, 2001a), Schneider (1996a), Stevenson & Loconte (1996), and Schneider & al. (in prep.) have increased support for the molecular-based consensus topology. For eusporangiate and basal leptosporangiate ferns, evidence is now sufficient to allow us to circumscribe confidently most clades and assign ranks. However, for some more derived leptosporangiate ferns, the phylogenetic evidence is still somewhat equivocal. Consequently, declaration of phylogenetic positions for some taxa and the assignment of ranks (which we consider subjective and secondary), in a classical “Linnaean-style” hierarchy, are tentative. In this paper, we present a revised view of the classification of extant ferns, taking into account all relevant evidence. We focus our classification at the ranks of class, order, and family, believing that the information at hand is most appropriate for resolution and understanding of relationships at these levels. Within most families, and especially at the generic level, there is still insufficient evidence to attempt many classificatory decisions.

In the classification proposed herein, we account for, and place in a revised taxonomic framework, all names at family and ordinal rank utilized in previous major classifications directed at ferns, particularly those that have been proposed in the last eighty years: Bower (1926), Christensen (1938), Ching (1940, 1978), Dickason (1946), Copeland (1947), Holtum (1947, 1949, 1973), Pichi Sermolli (1958, 1977), Mehra (1961), Wagner (1969), Nayor (1970), Tagawa & Iwasuki (1972), Mickel (1974), Tryon & Tryon (1982), Kramer (in Kubitzki, 1990), Hennipman (1996), and Stevenson & Loconte (1996). We also consider various herbarium schemes in common use, such as the one by Crabbe & al. (1975). Many of these classifications, as well as others, have been reviewed and reproduced by Pichi Sermolli (1973), who also summarized detailed information on family names of ferns (1970, 1981, 1982, 1986). Smith (1995) provided a recent summary and discussion of these classifications.

Classifications serve many purposes, among them to provide a genealogical framework in which to identify plants, organize herbaria, retrieve information, and to conduct many kinds of studies (e.g., evolutionary, morphological, and physiological). Multi-use classifications serve us best if we name only those clades that are readily recognizable and characterized by morphological synapomorphic characters, at least at family and higher ranks. However, more traditional (morphology-based) and practical classifications are sometimes incompatible with the results and classifications implied by phylogenetic studies, especially when the principle of monophyly is used as a grouping criterion (recognizing clades, and not paraphyletic grades; APG II, 2003). When a traditionally recognized family nests within another, complex classificatory choices ensue: (1) recognition of paraphyletic families (Brummitt, 1996, 1997; Lidén & al., 1997; Moore, 1998; Diggs & Lipscomb, 2002; Grant, 2003); (2) dismemberment of a recognized family into smaller families (e.g., the disintegration of classical Scerophulariaceae; Olmstead & al., 2001); or (3) integration of the traditional family that causes the paraphyly into the “progenitor” family. The first choice, preferred by some, leads to recognition of unnatural (non-morphogenetic) groups, which in our opinion often retards or obscures investigation into interesting biological, phytogeographic, and evolutionary questions. The second solution supposes that we have morphological synapomorphies for nodes that lead to all of the segregate families, and this is not often the case, although one hopes that eventually we shall find these synapomorphies. Until then, it may be nearly impossible to define some segregate families in such a way that they would be both keyable and circumscribable. The third solution is a “fast fix” to the problem, but expediency often demands that at least some of the intrafamilial subclades also be recognized taxonomically, either at a lower rank (e.g., subfamily), or with an unranked informal name (e.g., “grammitid ferns”) until further decisions on rank can be made. This third option seems to us the most practicable and practical solution toward a “first-pass” revision of fern classification. As more data are gathered and future phylogenetic analyses provide better resolved and better supported topologies, one expects further insight into identifying synapomorphies for segregate taxa, enabling eventual movement toward the second option of recognizing segregate monophyletic families.

The nested linearity of a ranked Linnaean classification and the availability of a limited number of universally accepted ranks facilitate the organization and arrangement of taxa for cataloging purposes, such as the efficient arrangement of specimens in herbaria or the organization and retrieval of regional biodiversity from checklists, floras, and other taxonomic products. Ranked classifications often perform poorly, however, when called upon to present explicit statements of clade membership and relationship. Such classifications also can mislead one into making spurious comparisons, e.g., attempting to describe the extent of biodiversity in terms of
numbers of taxa of a particular arbitrarily designated rank (comparing apples with oranges). Such problems notwithstanding, it is nevertheless likely that ranked Linnaean classifications will continue to co-exist with phylogenetic classifications for the foreseeable future.

In this paper we combine the principle of monophyly with a desire 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. However, we attempt to avoid recognizing monogenic families within the more derived leptosporangiate ferns. To paraphrase Crisp & al. (1999), who addressed the matter of monotypic genera, the most compelling case for recognizing a monotypic family is when such a family is characterized by one or more autapomorphies and is the sister group to a clade of families, all of the members of which lack these apomorphies. The alternative would be to treat the whole clade (including the autapomorphic family) as a single family, which results in sinking some well-circumscribed families into synonymy. At this time, we prefer to utilize a minimum number of ranks to categorize only the most well supported splits in the phylogeny.

In some respects, our new classification differs in relatively minor ways in the circumscription of orders, families, and hierarchical structure from most other recent fern classifications (e.g., those of Tryon & Tryon, 1982; Kramer, in Kubitzki, 1990; and Stevenson & Loconte, 1996), but there are significant departures. Only one previous fern classification has employed cladistic methodology in a rigorous way; Stevenson & Loconte (1996) superimposed on their tree a hierarchical classification (albeit somewhat abbreviated), but the phylogeny that they generated was based exclusively on morphological data and differs radically from the most up-to-date phylogenetic hypothesis. Our classification, in contrast, is based on consensus of a variety of morphological and molecular studies.

Fern names above the rank of genus used in this classification (Appendices 1–4) have been obtained, for the most part, from the web site of James Reveal, University of Maryland (http://www.life.umd.edu/emeritus/reveal/PBIO/fam/hightaxindex.html) and from Hoogland & Reveal (2005). 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). To the best of our knowledge (and unless otherwise indicated), the family names in Appendix 3 have all been published in accord with the International Code of Botanical Nomenclature (Greuter & al., 2000) and thus satisfy the relevant Articles in the Code with regard to publication and priority of family names (Art. 10.6, Art. 11.1–11.3; Art. 18; Art. 41.1) and names of ranks above family (Art. 16, 17). Although the principle of priority is not mandatory for names of taxa above the rank of family (Art. 11.9), authors are advised to follow this principle (Rec. 16B.1). Of the orders we recognize below, all have priority except Salviniales, which is later than the much less commonly applied name Pilulariales.

The rules of nomenclature applicable to supra-ordinal names are the same as those for ordinal names, discussed above. We have made no attempt to scrutinize the literature for names above the rank of order, but many of these names are included in lists available from the Reveal website (and so are included in Appendix 1) and in Hoogland & Reveal (2005); still others can be gleaned from Kenrick & Crane (1997, see, especially, their Table 7.2, pp. 231–233; however, many of these are not validly published) and from Pichi Sermolli (1959). Names at ordinal and subordinal ranks, also mostly from the Reveal website and from Hoogland & Reveal (2005), are given in Appendix 2, names at familial rank are given in Appendix 3. Citations for all names are given in Appendix 4. We also present an index to commonly accepted genera with family assignments proposed here (Appendix 5).

In the classification that follows, for each family, we give common names (often derived from the scientific names) for the clades (if there is one that has common usage), heterotypic synonyms, approximate numbers of genera and species, names of constituent genera, references to relevant phylogenetic literature, and discussion of unresolved problems, where appropriate. DNA sequence data are now available for all families recognized herein, 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 and we are relatively confident in the placement of the genus. The classification presented below is based on the consensus relationships depicted in Fig. 2, which are derived from, and guided by, recent and ongoing phylogenetic studies (e.g., Hasebe & al., 1995; Pryer & al., 2004b; Schneider & al., 2004d; Korall & al., 2006; Schuettpeitz & al., 2006, unpubl. data).

CLASSIFICATION OF EXTANT FERNS

In this reclassification, we treat all classes, orders, and families of extant ferns, which constitute a mono-
Phylectic group, sometimes referred to as Infradivision Moniliformopses (Kenrick & Crane, 1997), or moniliphytes (Donoghue in Judd & al., 2002; Pryer & al., 2001a, 2004a, b). However, “Infradivision” is not a recognized rank in the International Code of Botanical Nomenclature (Greuter & 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 at an appropriate rank are not available for ferns (as here defined), euphyllophytes (ferns + seed plants), or even vascular plants (euphyllophytes + lycophytes), and because all available names at higher ranks have been used in a sense we think would be confusing, we avoid placing ferns in any rank above class. Classification may be better served by adopting “floating”, rankless names for clades above the rank of class.

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

I. CLASS PSILOTOPSIDA

A. ORDER OPHIOGLOSSALES.

1. Family Ophioglossaceae. — Ophioglossoids; incl. Botrychiaceae, Helmithostachyaceae. Four genera: Botrychium (grapeferns; moonworts), Helmithostachys, Mankuya, 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 & al., 2003). Ca. 80 spp.; monophyletic (Hasebe & al., 1995; Hauk, 1995; Pryer & al., 2001a, 2004b; Hauk & al., 2003). Mankuya, from Cheju Island, Korea, has recently been described, but no molecular data are available (Sun & al., 2001). Species mostly terrestrial (a few epiphytic), temperate and boreal, but a few pantropical. Characters: vernation nodding (not circinate); rhizomes and petioles fleshy; root hairs lacking; spores globose-tetrahedral, trilette; 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; spores reineform, monolete, 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 total spp. (2 in Psilotum); monophyletic (Hasebe & al., 1995; Pryer & al., 2001a, 2004). Characters: roots absent; stems bearing reduced, unveined or single-veined euphyls; 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 spp. usually placed in two well-marked subgenera, subg. Equisetum and subg. Hippochaete; monophyletic (Pryer & al., 2001a, 2004b; Des Marais & al., 2003; Guillon, 2004). The spermatozoids of Equisetum share several important features with other ferns that support their inclusion in this clade (Renzaglia & al., 2000). Kato (1983) added additional morphological characters, including root characters, supporting a relationship between horsetails and ferns. Characters: stems whorled, lacunate; leaves whorled, connate; sporangia with helical secondary wall thickenings (Bate man, 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. — Including Christenseniaceae.

4. Family Marattiaceae. — Marattioids; incl. Angiopteridaceae, Christenseniaceae, Danaeaceae, Kaulfiussiaceae. Four genera: Angiopteris, Christensenia, Danaea, Marattia; Archangiopteris has been recognized by some (e.g., Pichi Sermolli, 1977) but appears to nest within Angiopteris (Murdock, 2005); Danaea is sister to the other three genera (Pryer & al., 2001a, 2004b; Murdock, 2005) and represents a neotropical radiation (Christenhusz & al., unpubl.); Angiopteris and Christensenia are restricted to eastern and southeastern Asia, Australasia, and Polynesia, while Marattia is pantropical. Ca. 150 spp., but monographic revision is needed at the species level in several genera; monophyletic (Hill & Camus, 1986; Pryer & al., 2001a, 2004b; Murdock, 2005). We see no advantage or good reason for recognizing several of the constituent genera as monogenic families, as done by Pichi Sermolli (1977). The name Danaeaceae has been found to predate Marattiaceae (Appendix 4); however, Marattiaceae is being proposed for conservation by Murdock & al. (subm.), 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 separate; roots, stems, and leaves with mucilage canals; rhizomes fleshy, short, upright or creeping, with a polycy-
clic dictyostele; vernation circinate; leaves large, fleshy, 1–3-pinnate (rarely simple in Danaea, or 3–5-foliate 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; pneumatodes (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. — Three genera: Lepotopterus, Osmunda, Todea. Ca. 20 spp.; monophyletic (Hasebe & al., 1995; Yatabe & al., 1999; Pryer & al., 2001a, 2004b). Fossils from Permian; temperate and tropical. Characters: stem anatomy distinctive, an eutrophic 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; sporangiophores, with 128–512 spores, opening by an apical slit, annulus lateral; spores green, subglobe, trilette; gametophytes large, green, cordate, surficial; $x = 22$.

F. ORDER HYMENOPHYLLALES.

6. Family Hymenophyllaceae. — Filmy ferns; incl. Trichomanaceae. Nine genera (Ebihara & al., 2006), two major clades (Pryer & al., 2001b), “trichomanoid” and “hymenophyllid”, roughly corresponding to the classical genera Trichomanes s.l. and Hymenophys- lum s.l. Ca. 600 spp.; monophyletic (Hasebe & al., 1995; Dubuisson, 1996, 1997; Pryer & al., 2001b, 2004b; Ebihara & al., 2002, in press; Dubuisson & al., 2003; Hennequin & al., 2003). Several segregate and monotypic genera are nested within Hymenophysllum s.l.: Cardiomanes, Hymenoglossum, Rosenstockia, and Serpyllopsis (Ebihara & al., 2002, in press; Hennequin & al., 2003). Several other classically defined hymenophyllid genera (subgenera) may not be monophyletic, e.g., Mecodium and Sphaerocionium (Hennequin & al., 2003; Ebihara & al., 2006). Microtrichomanes appears to be polyphyletic (Ebihara & al., 2004). Trichomanes s.l. comprises eight monophyletic groups that are regarded here as genera: Abrodictyum s.l., Callistopteris, Cephalomanes, Crepidomanes, Didymoglossum, Polyplebiurn, Trichomanes s.s., and Vandenboschia; several of these have been subdivided into putatively monophyletic subgenera and sections (Ebihara & al., in press). Terrestrial and epiphytic; pantropical and south-temperate, but gametophytes survive in north-temperate regions as far north as Alaska. 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 (bivalve), with receptacles (at least in trichomanoid genera) usually elongate, protruding from the involucres; sporangia maturing gradually in basipetal fashion, each with an uninterrupted, oblique annulus; spores green, globose, trilette; 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. — Including Dipteridales, Matoniales, Stromatopteridales. Monophyletic (Pryer & al., 2004b; Schuettpelz & al., 2006). Characters: root steles with 3–5 protoxylem poles (Schneider, 1996a), antheridia with 6–12 narrow, twisted or curved cells in walls.

7. Family Gleicheniaceae. — Gleichenioids, forking ferns; incl. Dicranopteridaceae, Stromatopteridaceae. Six genera (Dicranopteris, Diplopterygium, Gleichenella, Gleichenia, Sticherus, Stromatopteris), ca. 125 spp.; monophyletic (Hasebe & al., 1995; Pryer & al., 1995, 2001a, 2004b). Hennipman (1996) also suggested inclusion of the next two families in Gleicheniaceae; however, these are recognized here 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. — Including Cheiroleprieaceae. Two genera, Cheirolepria and Dipteris, from India, southeast Asia, eastern and southern China, central and southern Japan, and Malesia, to Melanesia and western Polynesia (Samoa), ca. 11 spp.; monophyletic (Kato & al., 2001; Pryer & 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 exin-
dusiate, 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 4-seriate stalk; annuli almost vertical or slightly oblique; spores ellipsoid and monolete, or tetrahedral and trilete, 64 or 128 per sporangium; gametophytes cortade-thalloid; \( x = 33 \).

*Dipteris* differs from *Cheiropleuria* primarily in having bilateral, monolete sporangia (tetrahedral and trilet in *Cheiropleuria*) and monomorphic leaves with discrete sori (sporangia acrostichoid in *Cheiropleuria*).

9. **Family Matoniaceae.** — Matonioids. Two genera (*Matonia, Phanerosorus*), each with two spp.; monophyletic, sister to Dipteridaceae (Kato & Setoguchi, 1998; Pryer & al., 2004b; Schuettpelz & 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 pellate indusia; sporangia maturing simultaneously, with very short stalks and oblique annuli; spores globose-tetrahedral, trilet; gametophytes green, thalloid, with ruffled margins; antheridia large, many-celled; \( x = 26 \) (*Matonia*), 25 (*Phanerosorus*).

H. **ORDER SCHIZAEALES.** — Monophyletic (Hasebe & al., 1995; Pryer & al., 2001a, 2004b; Skog & al., 2002; Wikström & al., 2002). 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 spp.; monophyletic (Skog & al., 2002; Wikström & al., 2002). Terrestrial, pantropical. Characters: rhizomes creeping, slender, prostelistic, 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 sori, each sporangium covered by an antrorse indusium-like subtending flange; spores 128–256 per sporangium, tetrahedral and trilette; gametophytes green, coricate, surficial; \( x = 29, 30 \).

11. **Family Anemiaceae.** — Including Mohriaeae. One genus (*Anemia*, incl. *Mohria*), ca. 100+ spp.; monophyletic (Skog & al., 2002; Wikström & al., 2002). Terrestrial; primarily New World, but a few spp. in Africa, India, and islands in 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 & Lugardon, 1991); gametophytes green, coricate, surficial; \( x = 38 \).

12. **Family Schizaeaceae.** — Two genera (*Actinostachys*, *Schizaea*), ca. 30 spp.; monophyletic (Skog & al., 2002; Wikström & al., 2002). The Cretaceous *Schizaeopsis* is the oldest fossil assigned to this lineage (Wikström & al., 2002). Terrestrial, pantropical. Characters: blades simple (linear) or fan-shaped, variously cleft and with dichotomous free veins; sporangia on marginal, elimate, branched or unbranched projections at blade tips, not in discrete sori, exdusiate; spores bilateral, monolete, 128–256 per sporangium; gametophytes green and filamentous (*Schizaea*), or subterrestrial and non-green, tuberous (*Actinostachys*), and non-green; a puzzling array of base chromosome numbers: \( x = 77, 94, 103 \).

I. **ORDER SALVINIALES.** — Water ferns, heterosporous ferns; incl. “Hydropteridales”, Marsileae, Pilulariales. Monophyletic (Hasebe & al., 1995; Pryer, 1999; Pryer & al., 2001a, 2004b). 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 total spp.; monophyletic (Hasebe & al., 1995; Pryer, 1999; Nagalingum & al., unpubl.). Hennipman (1996) included both Salviniaeae and Azollaceae within Marsileaceae, but the spores of Marsileaceae differ markedly from those of Salviniaeae and Azollaceae (Schneider & 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 & al., in press), these arising from the rhizomes or from the base of the petioles, one to many per plant; heterosporous, microspores globose, trilet, megaspores globose, each with an acrolamella positioned over the exine aperture (Schneider & Pryer, 2002); perine gelatinous; \( x = 10 \) (*Pilularia*), 20 (*Marsilea*).

14. **Family Salviniaeae.** — Floating ferns, mosquito ferns; incl. Azollaceae. Two genera (*Salvinia, Azolla*), ca. 16 spp.; monophyletic (Pryer & al., 1995, 2004b; Reid & al., 2006). Some authors separate the genera into two families (Schneller in Kubitzki,
1990). Plants free-floating, subcosmopolitan; fossil record beginning in Cretaceous (Collinson, 1996). Characters: rhizomes as- cending to erect, solenostelic, bearing runners, clothed with usually thick, bold, ± parallel, sometimes anasto- mosing ridges on the distal face; these ridges are the 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 spp. (Zhang & Nooteboom, 1998); monophyletic (Korall & al., 2006). Characters: rhizomes creeping to usually erect, lacking hairs or scales; leaves dimorphic; blades pectinate to 1-forked; 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?


One genus (Cibotium), ca. 11 species; monophyletic, with some affinity to Dicksoniaceae, as circumscribed here (Korall & al., 2006). Terrestrial, amphipacific (east- ern 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 peti- olar bases; fronds monomorphic, mostly 2–4 m long; petioles hairy at bases, with three corrugated vascular bundles arranged in an omega-shape; blades large, bipin- nate to bipinnate-pinnatifid or more divided; secondary and tertiary blade axes adaxially ridged; veins free, simple or forked to pinnate; stomata with 3 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, paraphy- ses filiform; spores globose-tetrahedral, with prominent angles and a well-developed equatorial flange; antheridi- al walls 5-celled; x = 68.

The spores of Cibotioideae are unlike those of all other families in Cyatheales (Gastony, 1982; Tryon & Lugardon, 1991), with a prominent equatorial flange, and with usually thick, bold, ± 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* also have a prominent equatorial flange but lack distal ridges (Tryon & Tryon, 1982; Tryon & Luardon, 1991). As far as is known, the chromosome base number of $x = 68$ for *Cibotium* is also unique in the tree fern clade. The Hawaian species have been extensively studied by Palmer (1994).

20. Family Cyatheaceae. — Cyatheoids, scaly tree ferns; incl. Alsophilaceae, Hymenophyllopsidaceae. Ca. five genera: *Alsophila* (incl. *Nephelea*), *Cyathea* (incl. *Cnemidaria, Hemitelia, Trichipteris*), *Gymnosphaera, Hymenophyllopsis, Sphaeropteris* (incl. *Fournierea*); 600+ spp.; monophyletic, together with Dicksoniaceae, Metaxyaceae, and Cibotiacae constituting the “core tree ferns” (Korall & al., 2006). Several studies have addressed relationships within Cyatheaceae (Conant & al., 1995, 1996; Hasebe & al., 1995; Stein & al., 1996; Lantz & al., 1999; Conant & Stein, 2001), and circumscriptions of genera have varied widely (e.g., Tryon, 1970; Holttum & Edwards, 1983). Several of these studies show convincingly that *Cnemidaria* nests within *Cyathea* (Conant & al., 1995; Conant & Stein, 2001; Korall & al., 2006). Hennipman (1996) included all other families here placed in Cyatheales (excepting Hymenophyllopisaceae, displaced 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, Guiana, northern Brazil). It has nearly always been regarded as an isolated genus in its own family (e.g., by Copeland, 1947; Tryon & Tryon, 1982). In the analysis by Wolf & al. (1999), a close relationship of *Hymenophyllopsis* to Cyatheaceae was suggested, based on a small taxonomic sampling. A larger sampling by Korall (in prep.) indicates that *Hymenophyllopsis*, as well as *Cyathea* and *Trichipteris*, all nest within *Cyathea*, and together form a well supported neotropical clade. The spores of *Hymenophyllopsis* are remarkably similar to some species of *Cyathea* (compare, e.g., Figs. 14.8–14.11 with 26.15–26.18 in Tryon & Tryon, 1982). Characters associating *Hymenophyllopsis* with Cyatheaceae include the presence of true scales on the rhizomes, petiole bases, and sometimes on the blades. Mostly arborescent, pantropical; fossils beginning in Jurassic or early Cretaceous. Characters: stems with polycyclic dictyostele, apices (and usually petiole bases) covered with large scales, sometimes also with trichomia (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 and completely surrounding sporangia, or bivalvate (*Hymenophyllopsis*); sporangia maturing gradately, with oblique annuli; receptacles raised; paraphyses usually present; spores tetrahedral, trilet, variously ornamented; gametophytes green, cordate; $x = 69$ (*Hymenophyllopsis* not yet counted).

21. Family Dicksoniaceae, nom. cons. — (Dicksonioids; incl. Lophosoriaeae). Three genera: *Calochaena, Dicksonia, Lophosoria*. Ca. 30 spp.; monophyletic (Korall & al., 2006). Terrestrial; eastern Asia, Australasia, Neotropics, St. Helena. Characters: mostly arborescent or with erect or ascending rhizomes; rizomes with polycyclic dictyostele, or solenostelic (*Calochaena*); 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 (*Calochaena, 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, trilet; $x = 56$ (*Calochaena*), 65 (*Dicksonia, Lophosoria*).

*Lophosoria* (3 spp.) is distinctive in having spores with a prominent subequatorial flange, with the proximal face coarsely tuberculate, the distal face perforate. It has often been recognized as comprising its own family, Lophosoriaeae (Pichi Sermolli, 1977; Tryon & Tryon, 1982; Kramer in Kubitzki, 1990).

22. Family Metaxyaceae. — A single genus (*Metaxya*), 2 spp.; monophyletic (Smith & al., 2001). Terrestrial, Neotropics. Characters: rhizomes short-creeping to ascending, dorsiventral, solenostelic, apices covered with pluricellular hairs; petioles each with an omegashaped, corrugated vascular bundle; blades simply pinnate; veins free, simple or forked at the base, ± 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, trilet; $x = 95, 96$.

K. ORDER POLYPODIALES. — Including “Aspidiales”, Aspleniaceae, Athyriaceae, Blechnales, “Davalliales”, Dennstaedtiales, Dryopteridales, Lindseaeales, Lorchitidales, Monachosorales, Negripteridales, Parkeriales, Platyzomatales, Pteridales, Saccolomatales, Thelypteridales. Monophyletic (Hasebe & al., 1995; Pryer & al., 1995, 2001a, 2004b; Schneider & al., 2004c). 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, Sphenomeris, Tapeinodium, Xyropoteris; in an unpublished thesis, Barcelona (2000) advocated the establishment of three additional genera allied to Odontosoria and Sphenomeris. Ca. 200 spp.; most likely monophyletic (Wolf & al., 1994; Pryer & al., 2004b; Korall & al., in press; Schuettpelz & al., in press). The inclusion of Lonchitis (traditionally associated with dennstaedtioid ferns) in Lindsaeaceae is puzzling on morphological grounds, but molecular evidence strongly suggests it belongs with the lindsaeoid ferns. Terrestrial, or infrequently epiphytic 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 soleno-stelic, 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 veinslets; 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, trilette, 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 (in Cyatheales), where it has historically been placed, e.g., by Kramer in Kubitzki, 1990; Stevenson & Loconte, 1996 (Korall & al., in press). Croft (1986) discussed its differences from dicksonioids and recognized it at family rank. A relationship to other lindsaeoids is suggested by the 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 & al., in press).

24. Family Saccolomataceae. — One genus, ca. 12 spp.; 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. Orthopteris) have been contentious. Kramer (in Kubitzki, 1990) treated Saccoloma as a subfamily within Dennstaedtiaceae. Terrestrial, pantropical. Characters: rhizomes short-creeping to erect and somewhat trunk-like (long-creeping in most Lind-saeaceae and Dennstaedtiaceae) and dictyostelic (usually soleno-stelic in Dennstaedtiaceae, protostelic with inter-nal phloem in Lind-saeaceae); petioles each with an omega-shaped vascular strand (open end adaxial); blades pinnate to decompound, 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 ± parallel, branched ridges; x = ca. 63.

25. Family Dennstaedtiaceae. — Dennstaedtioids; incl. Hypolepidaceae, Monachoraceae, Pteridiaceae. Ca. 11 genera: Blotiella, Coptodiateris, Dennstaedtia (incl. Costaria1), Histiopteris, Hypolepis, Leptolepia, Microlepis, Monachorus, Oenotrichia s.s.1, Pareia, Pteridium (bracken). Ca. 170 spp.; monophyletic, if lindsaeoid ferns are excluded (Pryer & al., 2004b; Schuettpelz & al., in press). Monachoraceae nests within Dennstaedtiaceae (Wolf & al., 1994; Wolf, 1995, 1997; Pryer & al., 2004b; Schuettpelz & al., 2006). Terrestrial, sometimes scandent; pantropical. Characters: rhizomes mostly long-creeping, often siphonostelic or poly-stelic, bearing jointed hairs; petioles often with epipetiolar buds, usually with a gutter-shaped vascular strand (open end adaxial); blades often large, 2–3-pinate or more divided; indument of hairs; veins free, forked or pinnate, rarely anastomosing and then without included veinslets; sori marginal or submarginal, linear or discrete, indusia linear or cup-like at blade margins, or reflexed over sori; spores tetrahedral and trilette, 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 pterido-ids; incl. Acrostichaceae, Actinopteridaceae, Adiantaceae (adiantoids, maidenhairs), Anopteraceae, Anaphy-aceae, Ceratopteridaceae, Cheilanthenaceae (cheilantheoids), Cryptogrammaceae, Hemionitidaceae, Negripteridaceae, Parkeriaceae, Platyzomataceae, Sinopteridaceae, Taeni-daceae (taenitidoids), Vittariaceae (vittarioids, shoestring ferns). Ca. 50 genera, 950 spp. Constituent genera, some of them notoriously polyphyletic or paraphyletic and in need of redefinition (e.g., Cheilanthes), include Acrostichum, Actinopteris, Adiantopsis, Adiantum, Aleur-itoperis, Ananthacorus, Anetium, Anogramma, Antheridium, Argyrochosma, Aspidotis, Astrolepis, Austrogramme, Bommeria, Cassebeera, Ceratopteris, Cerosora1, Cheilanthes, Cheliform, Coniogramme, Costentinia (Nakazato & Gastony, 2001), Cryptogramma, Doryopteris, Eriosorus, Haplotenteris, Hecestoperis, Hemionitidaceae, Holochoilaena, Jamesonia, Llavea, Mildella, Monogramma, Nephtoperis1, Neurocalis, Notholaena, Ochropteris, Onychium, Paraceterach, Parahemionitis, Pellaea (Kirkpatrick, unpubl.), Pentagramme, Pitrogramma, Platyloma, Platyzoma, Polystaenium, Pteris (incl. Afropoteris, Anopteris), Pirrozonium, Radiovittaria, Rheopteris, Scoliosorus, Syngramma, Taenitis, Trachypteris, and Vittaria. The family thus
defined is monophyletic (Gastony & Rollo, 1995, 1998; Hasebe & al., 1995; Pryer & al., 1995; Gastony & Johnson, 2001; Schneider & al., 2004c; Zhang & al., 2005). Pteridaceae comprises five monophyletic groups, 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 Parkerioidae (Acrostichum and Ceratopteris), (2) Adiantaceae, or Adiantoideae (Adiantum and the ten vittarioid genera; Crane & al., 1995; Hasebe & al., 1995; Hennipman, 1996; Crane, 1997; Huiet & Smith, unpubl.); (3) Cryptogrammaceae (comprising Coniogramme, Cryptogramma, and Llavea; Zhang & al., 2005), no subfamily name available; (4) Sinopteridaceae, or Cheilanthsioideae; and (5) Pteridaceae s.s., or Pteridoideae, containing Pteris (perhaps not monophyletic), its immediate allies, and the taenitioid ferns (Taenitis and allies; Sánchez-Baracaldo, 2004a, b).

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 decomposed; veins free and forking, or variously anastomosing and forming a reticulate pattern without included veins; 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, trilette, variously ornamented; mostly x = 29, 30.

Platyzoma, sometimes recognized as an isolated family, is aberrant in chromosome base number (x = 38; Tindale & Roy, 2002) and in having dimorphic spores (so-called “incipient heterospory”); Tryon, 1964), but nests with other genera of Pteridaceae, subfamily Pteridoideae (Hasebe & al., 1995; Pryer & al., 1995).

Ceratopteris (3 spp., monophyletic) nests within Pteridaceae in all molecular analyses, and it appears to be sister to Acrostichum (Hasebe & al., 1995; Pryer & al., 1995). It has a number of strong autapomorphies that separate it from other Pteridaceae: coarse 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, Anthrophyum, Haplopteris, Hecistopteris, Monogramma, Polystichum, Radiovittaria, Rheopteris, Scoliosorus, and Vittaria. The presence of Rheopteris in this clade is now clear (Huiet & Smith, unpubl.). 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 trilette, but reversals to the monolet 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 & al., 2003; Schneider & al., 2004b, 2005; Perrie & Brownsey, 2005). Regardless of the classification adopted, a huge majority of the species are in Asplenium, even if that genus is construed in a fairly strict sense; the segregate genera Camptosorus and Loxoscapho clearly nest within Asplenium s.l., or appear related to species heretofore generally placed in Asplenium (Murakami & al., 1999; Gastony & Johnson, 2001; Schneider & 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 & al., 1999; Pinter & al., 2002; van den Heede & al., 2003; Schneider & al., 2004b). One expects that the oft-recognized, but still unsampled genera Antigramma1, Holodictyum1, Schaffneria1, and Sinephropteris1 also nest in Asplenium Hymenasplenium, however, with a different chromosome base number than nearly all of the other segregates, as well as distinct root characters (Schneider, 1996b; Schneider & al., 2004b), appears to represent the sister clade to the rest of the species in the family, and this name could be adopted as a well-supported segregate genus. Ca. 700+ spp; monophyletic (Murakami & Schaal, 1994; Hasebe & al., 1995; Murakami & al., 1999; Gastony & Johnson, 2001; van den Heede & al., 2003; Schneider & al., 2004b, 2005; Perrie & Brownsey, 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 veins; 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, monolet, with a decidedly winged perine; x = 36 (mostly), but x = 38, 39 in Hymenasplenium (Murakami, 1995), 38 in Bonniella.

28. Family Thelypteridaceae. — Thelypteroids or thelypteridoids; incl. “Sphaerostephanaceae”. Circa
5–30 genera, depending on taxonomic viewpoint: commonly accepted segregates are Cyclosorus (incl. Ampelopteris, Amphineuron, Chingia, Christella, Cyclogramma, Cyclosorus s.s., Glaphyropteridopsis, Goniopterys, Meniscium, Menisorus, Mesophlebion, Pelazoneuron, Plesioneuron, Pneumatopteris, Pro nephrium, Pseudocyclosorus, Sphaeroestephano, Stegogramma, Steirop teris, Trigonospora), Macrothelypteris, Phegopteris, Pseudophegopteris, and Thelypteris (incl. Amauryperta, Coryphopteris, Metathelypteris, Oreopteris, Parathelypteris, and Thelypteris s.s.) (see Holtum, 1971; Smith & Cranfill, 2002). Ca. 950 spp.; monophyletic (Hasebe & al., 1995; Smith & Cranfill, 2002; Yatabe & al., 2002). Hennipman (1996) also included Blechnaceae and the athyrioid ferns in this family, a definition that would make Thelypteridaceae difficult or impossible to define morphologically.

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 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. Circa 15 genera as defined here, ca. 700 spp., nearly 85% of them in the two main genera, Athyrium and Diplazium (incl. Callipteris, Monomelangium), which are both probably paraphyletic (Wang & al., 2003). Other widely recognized genera include Acystopteris, Cheilanthopsis, Cornopteris, Cystopteris, Deparia (incl. Lunathyrium, Dryothyrium, Athyriopsis, and Dictyodroma; Sano & al., 2000b), Diplazium, Gymnocarpium (incl. Curania), Hemidictyum, Homalosorus, Protowoodsia, Pseudacystopteris, Rhachidosorus, and Woodsia (incl. Hymenocystis; see Shmakov, 2003). This family has been variously circumscribed, and its limits are still uncertain (Hasebe & al., 1995; Sano & al., 2000a, b). Wang & al. (2004) divided the Athyriaceae (excluding woodsiod ferns), by far the largest component in the family, into five subfamilies: Cystopteroidae, Athyrioidae, Deparioidae, Diplazioideae, and Rhachidosoroideae. As delimited here, the Woodsiaceae may be paraphyletic to the Aspleniaceae, Blechnaceae + Onocleaceae, and Thelypteridaceae, but support for this paraphyly—or alternatively for the monophyly of the family as here defined—is lacking in broad analyses (Hasebe & al., 1995; Sano & al., 2000a; Schneider & al., 2004c). 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. Further sampling will likely shed additional light on this subject, and the recognition of several additional families may be warranted.

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. Stenochlaenaaceae). Currently ca. nine genera recognized (Blechnum s.l., Brainea, Doodia, Pteridoblechnum, Sadleria, Salpichlaena, Steenisioblechnum, Stenochlaena, Woodwardia). Most of the existing recognized genera nest within Blechnum s.l., and their acceptance is dependent upon a revised recircumscription of Blechnum s.l., which is manifestly paraphyletic in its current usage (Nakahira, 2000; Cranfill, 2001). Ca. 200 spp.; monophyletic, sister to Onocleaceae (Hasebe & al., 1995; Cranfill, 2001; Cranfill & Kato, 2003). Woodwardia (incl. Archistea, Chieniopteris, Lorinersia) appears to be an early-branching member of the Blechnaceae (Cranfill & Kato, 2003). Characters: rhizomes creeping, ascending, or erect; scales at apices, 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 midrifs, indusiate, with linear indusia opening inwardly (toward midrifs); 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. 5 spp.; monophyletic, sister to Blechnaceae (Hasebe...
& al., 1995; Gastony & Ungerer, 1997). Family circumscriptio follows Pichi Sermolli (1977) and Gastony and Ungerer (1997, their tribe Onocleaee 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 laminal margins, also with membranous, often fugacious true indusia; x = 37 (Onoclea), 39, 40 (other genera).


Terrestrial, epipetric, hemiepiphytic, or epiphytic, pantropical, also with many temperate representatives. Characters: rhizomes creeping, ascending or erect, sometimes scendent 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 forked, free to variously anastomosing, with or without included veinlets; sori usually round, indusia round-reniform or peltate (lost in some lineages), or sori exindusiate, acrostichoid in a few lineages; sporangia with 3-rowed, short to long stalks; spores reniform, monolette, perine winged; x = 41 (nearly all genera counted), rarely 40 (presumably derived).

Dryopteridaceae, as defined here, is almost certainly monophyletic, if Didymochlaena, Hypodematum, and Leucostegia are excluded (Hasebe & al., 1995; Tsutsumi & Kato, 2006). 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 Hypodematum, 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 as close to Dryopteris (e.g., Tryon & Lugardon, 1991, using evidence from spore morphology). Leucostegia is nearly always placed in Davalliaceae (e.g., by Kramer, 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 & Lugardon, 1991), and x = 41 (vs. x = 40 in Davalliaceae). In a molecular phylogenetic analysis by Schneider & al. (2004c), Didymochlaena and Hypodematum were resolved as sister to one another, and together sister to the remainder of the Eupolypods I clade (Fig. 2), but support for these relationships was lacking. Tsutsumi & Kato (2006) found support for a sister relationship between Hypodematum and Leucostegia, and also support for these as sister to the remaining Eupolypods I, but Didymochlaena was unsampled in their analysis. Based on these results, we therefore believe it would be premature to segregate these genera from the Dryopteridaceae.

Within Dryopteridaceae, as defined here, nests Elaphoglossum (Hasebe & al., 1995; Sano & al., 2000a). Sometimes it is included in its own family Elaphoglossaceae, e.g., by Pichi Sermolli (1977), with 600–800 spp., many still undescribed. Elaphoglossaceae was regarded as comprising three genera by Pichi Sermolli (1977), but Microstaphyla and Peltapteris nest within Elaphoglossum (http://www.nybg.org/bsci/res/moran/elaphoglossum.html; Mickel & Atehortúa, 1980; Rouhan & al., 2004; Skog & 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 & al., 2001, 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 Onocleeae, as comprising a much larger family Dryopteridaceae s.l., with slightly varying circumscriptions (e.g., Tryon & Tryon, 1982; Kramer in Kubitzki, 1990; Wagner & 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.

### 33. Family Lomariopsidaceae. — Lomariopsids; incl. Nephrolepidaceae, sword ferns. Four genera: Cycloplepis, Lomariopsis, Nephrolepis, and Thysanosoria\(^1\); ca. 70 species. Characters: rhizomes creeping or sometimes climbing (plants hemiepiphytic); petioles with round vascular bundles arranged in a gutter-shape; blades 1-pinnate, pinnate entire or crenate, often articulate, auriculate in some genera; veins free, \(+\) 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, 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 Davidson & al., 1995) was constructed to comprise six genera (containing ca. 800+ species): Bolbitis (and segregates Edanyoa, Egenolfia), Elaphoglossum, Lomagramma, Lomariopsis, Teratophyllum, and Thysanosoria\(^1\). Based on available evidence, 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 spp., has sometimes been included in a monogenic family Nephrolepidaceae (Kramer in Kubitzki, 1990). It has been resolved and supported as sister to a large clade comprising the Tectariaceae, Oleandraceae, Polypodiaceae, and Davalliacae (Hasebe & al., 1995; Schneider & al., 2004); 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 & Kato, 2006) and therefore to be expunged from the Dryopteridaceae. Although we have here decided to tentatively include Nephrolepis in the Lomariopsidaceae, the monophyly of this clade requires additional scrutiny, and thus Nephrolepis may eventually require recognition.

### 34. Family Tectariaceae. — Tectarioids; incl. “Dictyoxiphiaceae”, “Hypoderriaceae”. 8–15 genera: Aenigmopteris\(^1\), Arthropteris, Heterogonium, Hypoderрис\(^1\), Pleocnema, Psammiosorus, Psomiocharpa\(^1\), Peridrys, Tectaria s.l. (incl. Amphliblestra\(^1\), Camptodium\(^1\), Chlamydogramme\(^1\), Cionium, Ctenitopsis, Dictyoxiphium, Fadienia, Hemigramma, Pleuroderris\(^1\), Pseudotectaria\(^1\), Quercifilix, and perhaps other genera mentioned above), and Triplophyllum (Holtum, 1986); ca. 230 species, most in Tectaria s.l. Generic limits, especially within Tectaria s.l., are still very much in doubt. The family appears monophyletic with the definition given. Including Tectariaceae within an expanded Dryopteridaceae renders the latter polyphyletic. Clenitis, Lastreopsis, and several other genera here included in Dryopteridaceae have often been considered closely related to tectarioid ferns (Pichi Sermolli, 1977; Holtum, 1986; Moran in Davidson & al., 1995), but molecular data suggest otherwise (Hasebe & al., 1995). 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 decompound; 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 dysploids 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 & al., 1995; Tsutsumi & Kato, 2006). Psammiosorus, a monotypic genus endemic to Madagascar, has in turn been placed close to Arthropteris (Kramer, in Kubitzki, 1990) or even within Arthropteris (Tryon & Lugardon, 1991, on the basis of the 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. Family Oleandraceae. — Monogenic, ca. 40 spp., sister to Davalliacae + Polypodiaceae (Hasebe & al., 1995; Schneider & al., 2004; Tsutsumi & Kato, 2006). Kramer (in Kubitzki, 1990), included two genera in addition to Oleandra: Arthropteris (ca. 12 spp.), 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 Davalliacae. — Davallioids; excl. Gymnogrammiitidae. 4–5 genera: Araioestegia, Davallia (incl. Humata, Parasorus, Scypharia), Davallodes, Pachypleuria; ca. 65 spp. Monophyletic, sister to Polypodiaceae (Hasebe & al., 1995; Ranker & al., 2004; Schneider & al., 2004d; Tsutsumi & Kato, 2005), but more information needed. Gymnogrammitis and Leucoxestegia are often included in Davalliacae but the former belongs in Polypodiaceae (Schneider & al., 2002b),
while the latter is seemingly allied to Hypodematium (Dryopteridaceae; Tsutsumi & Kato, 2005). Generic limits of Araio-stegia, Davallia, and Pachypleuris relative to each other are ill-defined, and all of these genera appear to be paraphyletic or polyphyletic (Tsutsumi & 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 reniform or lunate indusia (rarely forming a submarginal coenosorus in Parasoros); sporangia with 3-rowed, usually long stalks; annuli vertical; spores ellipsoid, monolette, yellowish to tan, perine various, but usually not strongly winged or cristate; gametophytes green, cor- date; \( x = 40 \).

37. Family Polypodiaceae. — Polypods; incl. Drynariaeae, Grammitidaceae (grammitids), Gymnogrammitidaceae, Loxogrammaceae, Platyceareae, Pleurisoriopsidaceae. Ca. 56 genera, ca. 1200 spp. Pan- tropical, a few temperate. Genera include Acrosorus, Adenophorus (Ranker & al., 2003), Aglaomorpha (incl. Photinopteris, Merinthosorus, Pseudodrynaria, Holostachyum; Janssen & Schneider, 2005), Arthromeris, Belvisia, Calymmodon, Campylopterus, Ceradenia, Chirop- teris (Kreier & Schneider, unpubl.), Chryso grammitis, Cochlidium, Colysis, Ctenopteris, Dicranoglossum, Dictymia, Drynaria (Janssen & Schneider, 2005), Enterosora, Goniophlebium s.l., Grammitis, Lecanopteris (Haufler & al., 2003), Lellingeria, Lemnaphyl- lum, Lepisorus (incl. Platygoria), Leptochilus, Loxo- gramme (incl. Anarthropilis, Pachypleuria), a monotype from New Zealand; Kreier & Schneider, in press), Melpomene, Microgramma (incl. Solanopteris), Micropolypodium, Microsorum, Neochilium (incl. Neolepisorus), Neurodium, Niphidium, Peculma, Phlebodium, Phym atosorus, Platycerium (Kreier & Schneider, 2006), Pleopelitis, Polypodioides, Polypodium, Prosapta, Pyrosoria (incl. Drymoglossum), Scleroglossum, Sel linguea (incl. Cryptophila, Polypodioperis), Serpocaulon (Smith & al., in press), Synnemia (Schneider & al., 2006), Terpsichore, Themelium, Thylactopteris (Schnei- der & al., 2004a), and Zygophlebia. Additional mono- typic genera, include Caobangia, Drymotaenium, Gymnogrammitis, Kontumia (Wu & al., 2005), Luismia, Pleuroseriopsis, and Podosorus.

Polypodiaceae s.s., as often recognized (e.g., by Kramer in Kubitzki, 1990), is paraphyletic, because it excludes the grammitids, and is generally segregated as Grammitidaeae (Ranker & al., 2004; Schneider & al., 2004d). Gener- neric boundaries need clarification, and, in particular, Polypodium and Microsorum, two of the largest assemblies, are known to be polyphyletic (Schneider & al., 2004d). Certain previously misplaced genera are now shown to be nested within Polypodiaceae, e.g., Pleuro- soriopsis (Hasebe & al., 1995, Schneider & al., 2004d) and Gymnogrammitis (Schneider & al., 2002b). Polypodiaceae contains large wholly Neotropical and wholly Paleotropical clades (Schneider & al., 2004d).

Mostly epiphytic and epipetric, a few terrestrial; pantropical. Characters: rhizomes long-creeping to short- cresting, dictyostelic, bearing scales; petioles cleanly abscising near their bases or not (most grammitids), leaving short phyllodia; 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 including veins, 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, Pleopelitis); sporangia with 1–3-rowed, usually long stalks, frequently with paraphyses on sporangia or on receptacle; spores hyaline to yellowish, reniform, and monolette (non-grammitids), or greenish and globose-tetrahedral, trilet (most grammitids); perine various, usually thin, not strongly winged or cristate; mostly \( x = 35, 36, 37 \) (25 and other numbers also known).

Within Polypodiaceae, as defined above, nest the grammitid ferns (Ranker & al., 2004; Schneider & al., 2004d). Tryon & Tryon (1982) and Hennipman (1996) subsumed the grammitids in Polypodiaceae, as we do here. Grammitids (ca. 20 genera, 600 species, pantropical) do share a large number of morphological synapo- morphies: veins free (mostly); scales lacking on blades; setiform, often dark red-brown hairs on leaves; sporan- gial stalks 1-rowed; spores green, trilet; gametophytes ribbon-shaped. Some genera of grammitids have now shown to be polyphyletic, e.g., Ctenopteris, Gram- mitis, Micropolypodium, and Terpsichore, while others are likely monophyletic, e.g., Ceradenia, Melpomene, Prosapta s.l. (Ranker & al., 2004).

ACKNOWLEDGEMENTS

The authors thank Ray Cranfill for comments on an early draft of the manuscript. We also thank Chie Tsutsumi and Masahiro Kato, for sharing a pre-publication copy of their paper on Davalliaeae and related genera, and two anonymous reviewers, for providing helpful comments. James Reveal kindly provided comments and suggestions on nomenclatural aspects of our
work, especially information summarized in appendices. Our work was supported in part by National Science Foundation grants DEB-9616260 to ARS; DEB-9615533, DEB-0088900, and DEB-0347840 to KMP, DEB-9707087 to PGW, and DEB-0408077 to ES; a postdoctoral fellowship from the Swedish Research Council (2003-2724) to PK; and a German Science Foundation grant SCHN 758/2-1 to HS.

LITERATURE CITED


Press, Washington, D.C.


Tryon, R. M. & Tryon, A. F. 1982. Ferns and Allied Plants, with Special Reference to Tropical America. Springer-Verlag, Berlin.


**Appendix 1. Supra-ordinal names applied to extant ferns. Boldface indicates names adopted in this classification. * refers to Kenrick & Crane, 1997.**

<table>
<thead>
<tr>
<th>Subclass Blechnidae Doweld</th>
<th>Subdivision Ophioglossophytina Doweld</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subclass Cyatheidae Doweld</td>
<td>Class Ophioglossopsida Thomé</td>
</tr>
<tr>
<td>Class Cyatheopsida Doweld</td>
<td>Class Osmundopsida Doweld</td>
</tr>
<tr>
<td>Subclass Dennstaedtiidae Doweld</td>
<td>Subclass Plagiogyriidae Doweld</td>
</tr>
<tr>
<td>Subclass Equisetidae Warming</td>
<td>Subclass Polyподophyllidae* Cronquist, Takht. &amp; Zimmerm.</td>
</tr>
<tr>
<td>Division Equisetophyta D. H. Scott</td>
<td>Division Polyподophyllidae Cronquist, Takht. &amp; Zimmerm.</td>
</tr>
<tr>
<td>Subdivision Equisetophytina Reveall</td>
<td>Subdivision Polyподophyllina Reveall</td>
</tr>
<tr>
<td><strong>Class Equisetopsida</strong>* C. Agardh</td>
<td><strong>Class Polypodiopsida</strong> Cronquist, Takht. &amp; Zimmerm.</td>
</tr>
<tr>
<td>Subclass Filicidae Hook. &amp; Arn., nom. illeg.</td>
<td>Subclass Psilotidae Reveall*</td>
</tr>
<tr>
<td>Division <em>Fилиcophylla</em> J. Mackay, nom. illeg.</td>
<td>Division Psilotopphyta Heintze</td>
</tr>
<tr>
<td>Class <em>Fилиcopsida</em> C. Agardh, nom. illeg.</td>
<td>Subdivision Psilotophytina Tippo ex Reveall</td>
</tr>
<tr>
<td>Subclass Gleichenididae Doweld</td>
<td><strong>Class Psilotopsida</strong>* D. H. Scott</td>
</tr>
<tr>
<td>Class Gleicheniopsida Doweld</td>
<td>Subclass Pterididae Schmakov</td>
</tr>
<tr>
<td>Class Hymenophyllopsida Doweld</td>
<td>Subkingdom Pteridobiotina Underw.</td>
</tr>
<tr>
<td>Subclass Marattiidae Klinge</td>
<td>Division Pteridophyta Schimp.</td>
</tr>
<tr>
<td>Division Marattiophyta Heintze</td>
<td>Superdivision Pteridophytanae Doweld</td>
</tr>
<tr>
<td>Class Marattiopsida Doweld</td>
<td>Subdivision Pteridophytina Engl.</td>
</tr>
<tr>
<td>Subclass Marsileididae Doweld</td>
<td>Class Pteridopsida Ritgen</td>
</tr>
<tr>
<td>Class Marsileopsida Trevis.</td>
<td>Subclass Salviniidae Cronquist, Takht. &amp; Zimmerm. ex Reveall</td>
</tr>
<tr>
<td><strong>Class Matoniopsida</strong> Doweld</td>
<td>Subclass Salviniopsida Kamelin &amp; Schmakov</td>
</tr>
<tr>
<td>Subclass Matonididae Doweld</td>
<td>Subclass Schizaeeidaceae Doweld</td>
</tr>
<tr>
<td>Infradivision <em>Moniliformium</em>, nom. illeg.</td>
<td>Class Schizaeeopsida Doweld</td>
</tr>
<tr>
<td>Subclass Ophioglossidae* Klinge</td>
<td>Class Schizaeeopsida Doweld</td>
</tr>
<tr>
<td>Division Ophioglossophyta Bek.</td>
<td>Division Ophioglossophyta Bek.</td>
</tr>
</tbody>
</table>
Appendix 2. Ordinal and subordinal names applied to extant ferns. In this list, an equal sign (=) indicates that we regard the first name as a synonym of the one we adopt. * refers to orders adopted by Pichi Sermolli (1977); most of these names are not validly published. Boldface indicates orders adopted in our classification. A name in quotes indicates that it is not validly published.

Order “Aspidiales”; used by various authors, e.g., Pichi Sermolli (1958, 1977), nom. illeg. = Polypodiales
Order Aspleniales Pic. Serm. ex Reveal = Polypodiales
Order Athyriales Schmakov = Polypodiales
Order Blechnales Pic. Serm. ex Reveal = Polypodiales
Order Christenseniiales Doweld = Marattiaceae

Order Cyatheales A.B. Frank
Suborder Cyatheinae Bessey
Order “Davalliales”, nom. illeg. = Polypodiales
Order Dennstaedtiiales Doweld (name also used by Pichi Sermolli, 1977, where it is a nom. nud.) = Polypodiales
Order Dicksoniales Pic. Serm. ex Reveal = Cyatheales
Order Dipteridales Doweld = Gleicheniales
Order Dryopteridales Schmakov = Polypodiales

Order Equisetales DC. ex Bercht. & J. Presl
Suborder Equisetinae Rabenh.
Order Filicales Dumort., nom. illeg.

Order Gleicheniales* Link
Suborder Gleicheniinae Bessey
Order “Hydropteridales” (Hydropterides) used by many authors, e.g., Copeland (1947), Kubitzki (1990) = Salviniales

Order Hymenophyllales A.B. Frank
Suborder Hymenophyllinae Bessey
Order Hymenophyllopsidales Pic. Serm. ex Reveal = Cyatheales
Order Lindsesiales Doweld = Polypodiales
Order Lonchitidales Doweld = Polypodiales

Appendix 3. 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
Actinidiaceae Pic. Serm. = Pteridaceae
Adiantaceae Newman, nom. cons. over Parkeriaceae = Pteridaceae
Alsophiliaceae C. Presl = Cyatheaceae

Anemiaceae Link; here included in Schizaeaceae
Angiopteridaceae Fée ex J. Bommer = Marattiaceae
Anopteraceae Doweld = Pteridaceae
Antrophyaceae Ching = Pteridaceae
“Aspidiaceae” Burnett, nom. illeg. = Dryopteridaceae

Aspleniaceae Newman; here included in Polypodiales
Athyriaceae Alston = Woodsiaceae
Azollaceae Wettst. = Salviniales

Blechnaceae Newman; here included in Polypodiales
Bolbitidiaceae Ching = Dryopteridaceae
Botrychiaceae Horan. = Ophioglossaceae
Ceratopteridaceae Underw. = Parkeriaceae = Pteridaceae
Cheilanthes B.K. Nayar = Pteridaceae
Chiteriuaceae Nakai = Dipteridaceae
Christenseniaceae Ching = Marattiaceae

Chitoniaceae Korall; here included in Cyatheales
Cryptogrammaceae Pic. Serm. = Pteridaceae
Culcitaeeae Pic. Serm.; here included in Cyatheales

Cyatheaceae Kauff.; here included in Cyatheales
Cystodiaceae J.R. Croft = Lindsesaeae
Cystopteridaceae Schmakov
Danielaceae 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
“Dictyoxiphiaeae” Ching, nom. nud. = Tectariaceae
“Didymochnaeeae” Ching, nom. nud. = Dryopteridaceae, tentatively

Dipteridaceae Seward & 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

“Filiaceae” Juss., nom. illeg.

Gleicheniaceae C. Presl, here included in Gleicheniales
Grammitidaceae Newman [often misspelled Grammitaceae] = Polypodiaceae
Gymnogymnidiaceae Ching (incl. Gymnogymnaceae, spelling variant used by some authors) = Polypodiales
Helmintostachyaceae Ching = Ophioglossaceae
Hemionitidaceae Pic. Serm. = Pteridaceae

Hymenophyllaceae Mart.; here included in Hymenophyllales
Hymenophyllopsidaceae Pic. Serm. = Cyatheaceae
Hydropidaceae Ching = Dryopteridaceae, tentatively
“Hydopdriaeeae” Ching, nom. nud., used by various authors, incl. Dickason (1946) = Tectariaceae
Hypolepidaceae Pic. Serm. = Dennstaedtiaceae

Lindsaeaeae C. Presl; here included in Polypodiales
Lomariopsidaceae Alston; here included in Polypodiales
Appendix 3. Continued.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lonchitidaceae Doweld</td>
<td>= Lindsaeaceae</td>
</tr>
<tr>
<td>Lophosorinaeae Pic. Serm.; here included in Dicksoniaceae</td>
<td></td>
</tr>
<tr>
<td>Loxogrammaceae Ching ex Pic. Serm.</td>
<td>= Polypodiaceae</td>
</tr>
<tr>
<td>Loxomataceae C. Presl [often misspelled “Loxosomataceae”; here included in Cyatheales]</td>
<td></td>
</tr>
<tr>
<td>Lygodiaceae M. Roem.; here included in Schizaeales</td>
<td></td>
</tr>
<tr>
<td>Marattiaceae Kaulf., nom. cons. prop.; here included in Marattiales; antedated by Danaeaceae (Murdoch &amp; al., subm.)</td>
<td></td>
</tr>
<tr>
<td>Marsileaceae Mirb.; here included in Salviniales</td>
<td></td>
</tr>
<tr>
<td>Matoniaceae C. Presl; here included in Gleicheniales</td>
<td></td>
</tr>
<tr>
<td>Metaxyaceae Pic. Serm.; here included in Cyatheales</td>
<td></td>
</tr>
<tr>
<td>Mohriaceae C.F. Reed. = Anemiaceae</td>
<td></td>
</tr>
<tr>
<td>Monachosoraceae Ching = Dennstaedtiaceae</td>
<td></td>
</tr>
<tr>
<td>Negripteridaceae Pic. Serm.</td>
<td>= Pteridaceae</td>
</tr>
<tr>
<td>Nephrolepidaceae Pic. Serm. = Lomariopsidaceae, tentatively</td>
<td></td>
</tr>
<tr>
<td>Oeleandraceae Pic. Serm.</td>
<td>Here included in Polypodiales</td>
</tr>
<tr>
<td>Oncolaceae Pic. Serm.; here included in Polypodiales</td>
<td></td>
</tr>
<tr>
<td>Ophioglossaceae Martynov; here included in Ophioglossales</td>
<td></td>
</tr>
<tr>
<td>Osmundaceae Martynov; here included in Osmundales</td>
<td></td>
</tr>
<tr>
<td>Parkeriaceae Hook. = Pteridaceae</td>
<td></td>
</tr>
<tr>
<td>Peranemataceae (C. Presl) Ching</td>
<td>= Dryopteridaceae</td>
</tr>
<tr>
<td>Pilulariaceae Mirb. ex DC. (Pilulariae)</td>
<td>= Marsileaceae</td>
</tr>
<tr>
<td>Plagiogyriaceae Bower; here included in Cyatheales</td>
<td></td>
</tr>
<tr>
<td>Platyacaceae Ching</td>
<td>= Polypodiaceae</td>
</tr>
<tr>
<td>Platyzygopteraceae Nakai</td>
<td>= Pteridaceae</td>
</tr>
<tr>
<td>Pleurosoportidaceae Kurita &amp; Ikebe ex Ching</td>
<td>= Polypodiaceae</td>
</tr>
<tr>
<td>Polypodiaceae J. Presl; here included in Polypodiales</td>
<td></td>
</tr>
<tr>
<td>Psilotaceae J.W. Griff. &amp; Henfr.; here included in Psilotales</td>
<td></td>
</tr>
<tr>
<td>Pteridaceae E.D.M. Kirchn.; here included in Polypodiales</td>
<td></td>
</tr>
<tr>
<td>Pteridaceae Ching = Dennstaedtiaceae</td>
<td></td>
</tr>
<tr>
<td>Saccolomataceae Doweld; here included in Polypodiales</td>
<td></td>
</tr>
<tr>
<td>Salvinieaeae Martynov; here included in Salviniales</td>
<td></td>
</tr>
<tr>
<td>Schizaeales Kauf.; here included in Schizaeales</td>
<td></td>
</tr>
<tr>
<td>Sinopteridaceae Koidz., nom. rej. in favor of Adiantaceae</td>
<td>= Pteridaceae</td>
</tr>
<tr>
<td>“Sphaerostephanaceae” Ching, nom. nud.</td>
<td>= Thelypteridaceae</td>
</tr>
<tr>
<td>“Stenochlaeniaceae” Ching = Blechnaceae</td>
<td></td>
</tr>
<tr>
<td>Stromatopteridaceae Bierh. = Gleicheniaceae</td>
<td></td>
</tr>
<tr>
<td>Taenitidaceae Pic. Serm.</td>
<td>= Pteridaceae</td>
</tr>
<tr>
<td>Tectariaceae Panigrahi; here included in Polypodiales</td>
<td></td>
</tr>
<tr>
<td>Thelypteridaceae Pic. Serm.; here included in Polypodiales</td>
<td></td>
</tr>
<tr>
<td>Thysopteridaceae C. Presl; here included in Cyatheales</td>
<td></td>
</tr>
<tr>
<td>Trisetopteridaceae Nakai</td>
<td>= Psilotales</td>
</tr>
<tr>
<td>Trichomanaceae Burmeist. = Hymenophyllaceae</td>
<td></td>
</tr>
<tr>
<td>Vittariceaeae Ching</td>
<td>= Pteridaceae</td>
</tr>
<tr>
<td>Woodsiaceae Herter; here included in Polypodiales</td>
<td></td>
</tr>
</tbody>
</table>

Appendix 4. Familial, ordinal, and supra-ordinal names for extant ferns, with citations from Reveal & Doweld (subm.), as revised from Hoogland & Reveal (2005), to comply with the Vienna Code. Orthographic variations in spelling, in original references, are in quotation marks. *Italicized* names are not validly published. * refers to ordinal names used by Pichi Sermolli (1977), some of them unpublished, some published by earlier authorities. Commonly used “descriptive names” (Art. 16.1), e.g., Hydropterides, are also given, but no attempt has been made to include all such names, or to determine first usage; no good index is available for these.

- **Fam. Aspidiaceae** Pic. Serm., Webbia 17: 5. 31 Aug 1962.
- **Fam. Botrychiaceae** Horan., Char. Ess. Fam.: 15. 30 Jun 1847.
Appendix 4. Continued.

- Fam. Danaeaceae C. Agardh, Aphor. Bot. 117. 19 Jun 1822; nom. rej. prop. in favor of Marattiaceae, nom. cons. prop. (Murdock & al., subm.).
  
  
  
  
  
  
  
  
  
Appendix 4. Continued.

Division Marattiophyta Heintze, Compl. Fylog.: 22. 1927.
Infradivision Moniliformopsis Kenrick & P. Crane; nom. nud. in Kenrick & Crane, 1997.
### Appendix 4. Continued.

<table>
<thead>
<tr>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Family Schizaceae Schultes &amp; Schultes f., Schizaeaceae 1: 2. 1833.</td>
</tr>
<tr>
<td>Subfamily Schizaceae Schultes &amp; Schultes f., Schizaeaceae 1: 2. 1833.</td>
</tr>
<tr>
<td>Tribe Schizaceae Schultes &amp; Schultes f., Schizaeaceae 1: 2. 1833.</td>
</tr>
</tbody>
</table>

### Appendix 5. 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 in roman; synonyms in *italics*. Family numbers assigned in text.

<table>
<thead>
<tr>
<th>Abacopteris = Cyclosorus</th>
<th>Archangiopteris = Angiopteris</th>
<th>Ceterach = Aspleniurn</th>
<th>Cyathanum (20)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abrodictyum (6)</td>
<td>Argyrochosma (26)</td>
<td>Ceterachopsis = Asplenum</td>
<td>Cyclophyllophylum</td>
</tr>
<tr>
<td>Acrophoros (32)</td>
<td>Arthrorhizos (37)</td>
<td>Chelianthes (26)</td>
<td>Cyclophyllophylum</td>
</tr>
<tr>
<td>Acropocarpus (32)</td>
<td>Arthropteris (34)</td>
<td>Cheilanthopsis (26)</td>
<td>Cyclosorus (28)</td>
</tr>
<tr>
<td>Acrostichum (26)</td>
<td>Aspidotis (26)</td>
<td>Cheiloperia (8)</td>
<td>Cyrtogonellum (32)</td>
</tr>
<tr>
<td>Actinopteris (26)</td>
<td>Astropleura (27)</td>
<td>Cheirion (8)</td>
<td>Cyrtomium (32)</td>
</tr>
<tr>
<td>Actinostachys (12)</td>
<td>Astrolepis (26)</td>
<td>Chirioniopsis (26)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Actinopteris (29)</td>
<td>Aenigmopteris (34)</td>
<td>Cystis (36)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Adenophoros (37)</td>
<td>Adiantopsis (26)</td>
<td>Cystis (36)</td>
<td>Davalliaceae</td>
</tr>
<tr>
<td>Adiantopsis (37)</td>
<td>Aipteris (26)</td>
<td>Cystis (36)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Adiantum (26)</td>
<td>Azolla (14)</td>
<td>Cystis (36)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Aenigmopteris (34)</td>
<td>Belvisia (37)</td>
<td>Cystis (36)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Afropteris</td>
<td>Blechnum (30)</td>
<td>Chrysodendron (37)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Aglaomorpha (37)</td>
<td>Biotella (25)</td>
<td>Chrysodendron (37)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Aleuritopteris</td>
<td>Bolbitis (32)</td>
<td>Chrysodendron (37)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Allantodia = Diplazium</td>
<td>Bomeria (26)</td>
<td>Chrysodendron (37)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Alsothia (20)</td>
<td>Botrychium (1)</td>
<td>Chrysodendron (37)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Amauropelea = Thelypteris</td>
<td>Botrypus = Botrychium</td>
<td>Cystis (36)</td>
<td>Davallia (36)</td>
</tr>
<tr>
<td>Amelopteris = Cyclosorus</td>
<td>Brainsea (30)</td>
<td>Coniochloa (26)</td>
<td>Dictyophyllum</td>
</tr>
<tr>
<td>Amphiblistera = Tectaria</td>
<td>Callipteris = Diplazium</td>
<td>Coptophyllum (25)</td>
<td>Dictyophyllum</td>
</tr>
<tr>
<td>Amphioceneum = Cyclosorus</td>
<td>Callipteris (6)</td>
<td>Coptophyllum (25)</td>
<td>Dictyophyllum</td>
</tr>
<tr>
<td>Anaphycocarpus (26)</td>
<td>Calathus (21)</td>
<td>Coptophyllum (25)</td>
<td>Dictyophyllum</td>
</tr>
<tr>
<td>Anarthroptera = Loxogramme</td>
<td>Calymnodium (37)</td>
<td>Cernostoma (26)</td>
<td>Dictyophyllum</td>
</tr>
<tr>
<td>Anchistea = Woodwardia</td>
<td>Camptodium = Tectaria</td>
<td>Costaria = Dennstaedtia</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Antarctica = Aspleniurn</td>
<td>Camptosorus = Aspleniurn</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Anetum (26)</td>
<td>Campyleaenu = Asplenium</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Angiopteris (4)</td>
<td>Cephaloeca (37)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Anogramma (26)</td>
<td>Cephalea (37)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Anopteris = Pteris</td>
<td>Caspea (26)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Anthogramma = Aspleniurn</td>
<td>Cephaloeca (37)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Anthrophyton (26)</td>
<td>Ceradenia (37)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Arachnoides (32)</td>
<td>Ceratopteris (26)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
<tr>
<td>Araiostegia (36)</td>
<td>Cerosa (26)</td>
<td>Coveniella (32)</td>
<td>Didymoglossum (6)</td>
</tr>
</tbody>
</table>
Appendix 5. Continued.

Drynaria (37) Leucostegia (32) Ophioderma = Ophioglossum
Dryopteris (32) Lindseyae = Nephelepis Pteridium = Dryopteris
Echinodorus (32) Litobrochia = Pteris Orthopteris = Tectaria
Elliptochloa (32) Lloarea (26) Osundia (5) Pyrrosia = Tectaria
Emetasia (37) Lophospermum = Grammitis? Queraxys = Tectaria
Equisetum (3) Lomaria = Blechnum Rhenania = Tectaria
Eriocaulus (26) Lomariopsis = Osmunda Rhipheopteris = Tectaria
Ptilopteris = Monachorosum Xyropteris (23)
Leptophyllum = Arachniodes Onychium (26) Rostriochlaena = Hymenophyllum
Leptora (25) Ochroleuca = Pteris Sceptridium = Botrychium
Leproptila = Monachorosum Xyropteris (23)
Leptopteris (5) Oronchium (26) Schaffneria = Tectaria
Leptophyllum = Arachniodes Onychium (26) Selaginella (37)
Ptilopteris = Monachorosum Xyropteris (23)
Leptosa (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidodendron = Arachniodes Onychium (26) Selaginella (37)
Leptopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidoptera = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Leptopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum
Lepidopteris = Monachorosum Xyropteris (23)
Leptora (25) Ochroleuca = Pteris Sclerospora = Hymenophyllum