

A revised family-level classification for eupolypod II ferns (Polypodiidae: Polypodiales)

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Abstract We present a family-level classification for the eupolypod II clade of leptosporangiate ferns, one of the two major lineages within the Eupolypods, and one of the few parts of the fern tree of life where family-level relationships were not well understood at the time of publication of the 2006 fern classification by Smith & al. Comprising over 2500 species, the composition and particularly the relationships among the major clades of this group have historically been contentious and defied phylogenetic resolution until very recently. Our classification reflects the most current available data, largely derived from published molecular phylogenetic studies. In comparison with the five-family (Aspleniaceae, Blechnaceae, Onocleaceae, Thelypteridaceae, Woodsiaceae) treatment of Smith & al., we recognize 10 families within the eupolypod II clade. Of these, Aspleniaceae, Thelypteridaceae, Blechnaceae, and Onocleaceae have the same composition as treated by Smith & al. Woodsiaceae, which Smith & al. acknowledged as possibly non-monophyletic in their treatment, is circumscribed here to include only *Woodsia* and its segregates; the other “woodsoid” taxa are divided among Athyriaceae, Cystopteridaceae, Diplaziopsidaceae, Rhachidosoraceae, and Hemidictyaceae. We provide circumscriptions for each family, which summarize their morphological, geographical, and ecological characters, as well as a dichotomous key to the eupolypod II families. Three of these families—Diplaziopsidaceae, Hemidictyaceae, and Rhachidosoraceae—were described in the past year based on molecular phylogenetic analyses; we provide here their first morphological treatment.

Keywords Athyriaceae; *Diplazopsis*; ferns; *Rhachidosorus*; taxonomy; Woodsiaceae

■ INTRODUCTION

Despite intensive studies spanning the late 1930s to 1980s (Christensen, 1938; Ching, 1940, 1978a, b; Copeland, 1947; Holttum, 1947; Alston, 1956; Nayar, 1970; Pichi Sermolli, 1973; Sledge, 1973; Mickel, 1974; Tryon & Tryon, 1982; see Smith, 1995), evolutionary relationships within ferns remained obscure, and suprageneric treatments varied wildly. Holttum lamented in 1971 that “most family names of ferns have had such different meanings, as used by different authors, that such names are only intelligible if we associate them with the names of particular authors”. He suggested “in the meantime it would best serve the ultimate stability of nomenclature if we regard all family names of ferns as informal and tentative (which in fact they have always been)” (Holttum, 1971a). Thirty-five years later, Hennipman (1996) voiced a similar sentiment, that “modern higher classifications of ferns are a jungle for the user”. As recently as 1990, for example, the schizaeoid ferns (Schizaeales sensu Smith & al., 2006) and pteroid ferns (Polypodiales: Pteridaceae sensu Smith & al.,

2006) were hypothesized to be each other’s closest living allies (Tryon & al., 1990); current evidence, however, suggests these lineages shared a most recent common ancestor over 260 million years ago (Schuettpelz & Pryer, 2009, their table S3), and that pteroids are more closely related to other Polypodiales, the Cyatheales, and the Salviniiales (in total, the vast majority of ferns) than they are to the schizaeoids. Suprageneric fern classifications had fallen into such disrepute that some recent Floras avoided them altogether, opting instead to present genera in alphabetical order (e.g., Smith, 1981; Palmer, 2002; Mickel & Smith, 2004; Zuquim & al., 2008).

For nearly two decades, renewed investigations using molecular (Hasebe & al., 1994, 1995; Manhart, 1994, 1995; Wolf & al., 1994, 1998, 1999; Wolf, 1995, 1997; Kranz & Huss, 1996; Pahnke & al., 1996; Vangerow & al., 1999; Sano & al., 2000a; Wang & al., 2003; Pryer & al., 2004; Schneider & al., 2004b; Wikström & Pryer, 2005; Korall & al., 2006a, b; Schuettpelz & al., 2006; Schuettpelz & Pryer, 2007), morphological (Schneider, 1996; Stevenson & Loconte, 1996), and combined molecular and morphological data (Pryer & al., 1995, 2001) have yielded increased

support for the relationships that shape the major branches of the fern tree of life. In 2006, these phylogenetic hypotheses were consolidated and presented in a revised classification for ferns (Smith & al., 2006).

Smith & al. (2006) recognized a monophyletic Polypodiatales (“Polypods”) within which the majority of species fall into two large “eupolypod” clades, sister to each other and christened Eupolypods I and Eupolypods II, respectively (Fig. 1) (Schneider & al., 2004b). Together, the eupolypod lineages include nearly 6000 species—more than half of extant fern diversity. The large eupolypod clades had been hinted at, rather presciently, by earlier workers, including Sledge (1973, his Aspidiaceae and Athyriaceae approximate the Eupolypods I and II, respectively) and Mickel (1974, who grouped members of what are now called Eupolypods together in a “derived” position on his tree, Polypodiaceae being the chief exception). The existence of the eupolypod clade was further suggested by early molecular (Hasebe & al., 1994, 1995), morphological (Stevenson & Loconte, 1996), and combined analyses (Pryer & al., 1995). Schneider & al. (2004b) were the first to adopt the names Eupolypods I and II for these two clades, and it was not until the Smith & al. (2006) compilation that their composition was broadly understood.

As currently circumscribed, Eupolypods II is a large clade, comprising over 2500 species, including those associated with the large genera *Asplenium* (~700 spp.), *Cyclosorus* (~650 spp.), *Diplazium* (~400 spp.), *Athyrium* (~180 spp.), and *Blechnum* (~150 spp.; estimates from Kramer & Viane, 1990; Kramer & al., 1990a, b; Smith, 1990). It encompasses great morphological and ecological variation (Fig. 2), including taxa as disparate as the diminutive dry-rock dwelling *Asplenium tenerrimum* Mett. ex Kuhn, large arborescent tropical *Blechnum auratum* (Fée) R.M. Tryon & Stolze, high-arctic plants of *Woodsia glabella* R. Br. ex Richardson, and the temperate floodplain understory (and frequently sautéed) *Matteuccia*

struthiopteris (L.) Tod. Given its species richness, morphological disparity, and lack of historical recognition, it is not surprising that unequivocal morphological synapomorphies for Eupolypods II are lacking. However, some clear trends exist that are particularly useful for distinguishing Eupolypods II from Eupolypods I. Most eupolypod II taxa have two vascular bundles in the stipe (vs. many bundles in Eupolypods I), and many eupolypod II species have linear, indusiate sori (in the rare cases where members of Eupolypods I have linear sori, they are not indusiate; Fig. 3).

In their treatment of Eupolypods II, Smith & al. (2006) recognized not only that the backbone relationships within the clade were unresolved, but that Woodsiaceae as it was then circumscribed was possibly not monophyletic; the data then available did not support a monophyletic Woodsiaceae, but they also did not support any alternative set of relationships (Hasebe & al., 1995; Sano & al., 2000a; Pryer & al., 2004; Schneider & al., 2004b). In recognizing a potentially non-monophyletic Woodsiaceae, Smith & al. (2006) issued the caveat that, while “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” (Smith & al., 2006).

Further studies were rapidly forthcoming. In their 400-taxon, three-gene study, Schuettpelz & Pryer (2007) showed that three genera—*Cystopteris*, *Gymnocarpium*, *Hemidictyum*—tentatively placed in Woodsiaceae (Smith & al., 2006) were only distantly related to other members of Woodsiaceae sensu Smith & al. (2006). This general pattern—Woodsiaceae sensu Smith & al. (2006) not monophyletic and the backbone relationships within Eupolypods II only weakly supported—was also uncovered by the two-gene analyses of Wei & al. (2010), the three-gene analyses by Kuo & al. (2011), and the four-gene study of Li & al. (2011).

To directly address the composition of the major clades within Eupolypods II and the relationships among them, Rothfels & al. (2012) assembled an expanded molecular dataset (five plastid loci) for 67 eupolypod II species and 14 outgroup taxa. Their taxon sampling was designed to capture the deepest divergences across Eupolypods II and those within each major clade, as well as any potentially isolated lineages, as suggested by previous molecular (particularly Sano & al., 2000a; Tzeng, 2002; Schuettpelz & Pryer, 2007; Kuo & al., 2011) or morphological studies (chiefly Kato & Darnaedi, 1988; Wang & al., 2004). Although the results of Rothfels & al. (2012) were consistent with those of earlier studies, the more comprehensive taxon and data sampling provided higher levels of support for relationships and helped to resolve most of the taxonomic challenges in Eupolypods II. We base our classification on their inferred phylogeny (see Fig. 4), with the caveat that, like all phylogenetic studies of the Eupolypods II to date, their phylogeny is based solely on plastid data; no loci from the nucleus or mitochondrion were included. This classification is similar in outline to the linear sequence recently proposed by Christenhusz & al. (2011), but is further informed by the critical data of Kuo & al. (2011), Li & al. (2011), and Rothfels & al. (2012).

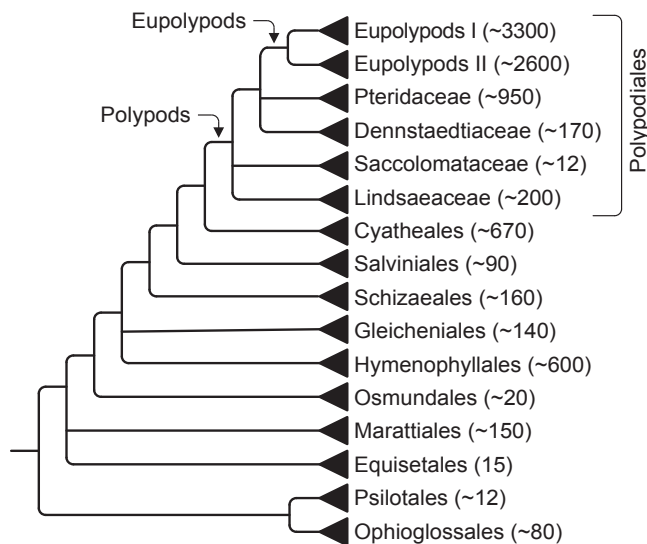


Fig. 1. Fern phylogeny. Numbers in parentheses indicate approximate species richness of each clade. Modified from Smith & al. (2006) and Rothfels & al. (2012).



Fig. 2. Representative eupolypod II ferns. Photographers are credited after the species names. ASPLENIACEAE—**A**, *Asplenium nidus* L. s.l. [M. Sundue]; **B**, *Asplenium montanum* Willd. [S. Zylinski]. ATHYRIACEAE—**C**, *Athyrium asplenioides* (Michx.) A.A. Eaton [S. Zylinski]. BLECHNACEAE—**D**, *Woodwardia areolata* (L.) T. Moore [C. Rothfels]; **E**, *Blechnum schomburgkii* (Klotzsch) C. Chr. [M. Sundue]. CYSTOPTERIDACEAE—**F**, *Gymnocarpium remotepinnatum* (Hayata) Ching [L.-Y. Kuo]; **G**, *Cystopteris protrusa* (Weath.) Blasdell [C. Rothfels]; **H**, *Cystopteris fragilis* (L.) Bernh. [C. Rothfels]. DIPLAZIOPSISIDACEAE—**I**, *Diplaziosis javanica* (Blume) C. Chr. [L.-Y. Kuo]. HEMIDICTYACEAE—**J**, *Hemidictyum marginatum* (L.) C. Presl [M. Sundue]. ONOCLEACEAE—**K**, *Onocleopsis hintonii* F. Ballard [C. Rothfels]; **L**, *Matteucia struthiopteris* (Hook.) Hayata [M. Sundue]. RHACHIDOSORACEAE—**M**, *Rhachidosorus mesosorus* (Makino) Ching [L.-Y. Kuo]. THELYPTERIDACEAE—**N**, *Thelypteris noveboracensis* (L.) Nieuwl. [C.W. Cook]. WOODSIACEAE—**O**, *Woodsia alpina* (Bolton) Gray [A. Larsson].

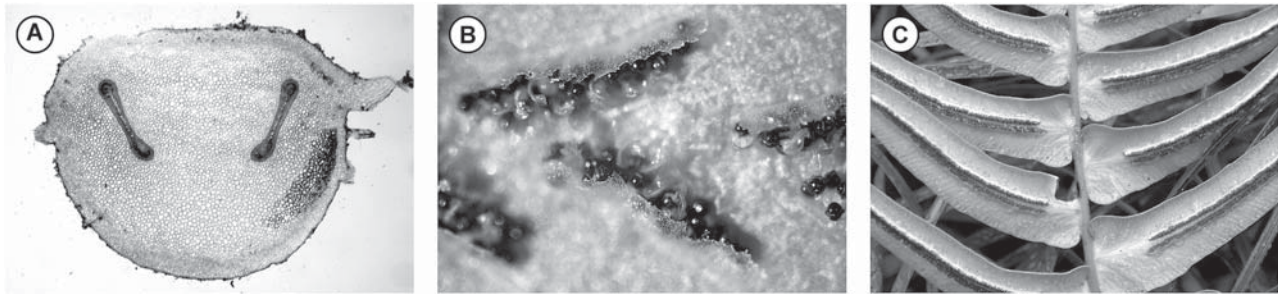


Fig. 3. Morphological characteristics of eupolypod II taxa. Photographers are credited within square brackets. **A**, Cross-section of *Diplaziopsis javanica* (Blume) C. Chr. (Diplaziopsidaceae) showing two vascular bundles at the base of the petiole [L.-Y. Kuo]. **B**, Close-up of abaxial leaf surface of *Asplenium platyneuron* (L.) Britton, Sterns & Poggenb. (Aspleniaceae), showing sporangia arranged in linear, indusiate sori. The sporangia are visible under the flap-like erose indusium, which opens away from the vein [C.J. Rothfels]. **C**, Abaxial leaf surface of *Blechnum occidentale* L. (Blechnaceae), again showing sporangia arranged in linear, indusiate sori. In this species the sori are contiguous along the main vein of each pinna, and the indusium opens towards the vein [R.C. Moran; modified with permission from www.plantsystematics.org].

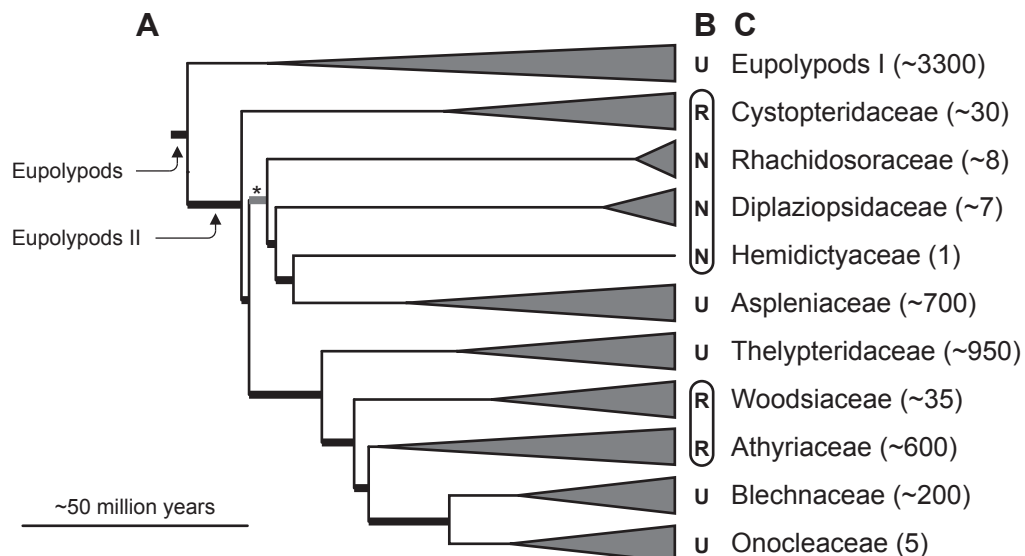


Fig. 4. Divergence and diversification in the Eupolypods II. **A**, Eupolypod phylogeny, with branch lengths approximately proportional to time (from the relaxed clock analyses of Rothfels & al., 2012, their Supplementary Fig. 1). The tip of the grey triangles along each branch marks the first sampled divergence within each family (Rothfels & al., 2012). All branches in this phylogeny are well supported (maximum likelihood bootstrap support $\geq 70\%$ and Bayesian posterior probability ≥ 0.95) with the exception of the grey branch, marked with an asterisk (*), which had 63% maximum likelihood bootstrap support and 0.89 posterior probability. **B**, Family-level nomenclatural status: N, newly described since Smith & al. (2006); R, recircumscribed (family name existed, but was not adopted by Smith & al., 2006); U, unchanged from Smith & al. (2006). Letters that are encircled indicate those families that have been segregated from Woodsiaceae sensu Smith & al. (2006). **C**, Family names, and approximate species richness, for the classification adopted here.

■ CLASSIFICATION OF THE EUPOLYPODS II

The aim of our classification is to recognize families within the eupolypod II phylogeny that balance the somewhat conflicting criteria of maximizing evolutionary informativeness (we thus adhere to the principle of monophyly) and minimizing nomenclatural instability (we retain long-established circumscriptions as much as possible). This conflict is most difficult to reconcile for *Asplenium* and its allies. Both choices (to recognize an expanded Aspleniaceae that includes *Hemidictyum*, *Diplaziopsis*, and *Homalosorus*, or to create new families

to accommodate the latter three genera) yield justifiable, monophyletic families. We take the latter approach—to recognize Aspleniaceae, Hemidictyaceae, and Diplaziopsidaceae—despite the addition of two small families, in order to preserve the long-standing use of Aspleniaceae in the more restricted sense, to highlight the deep divergence of each of the respective groups (Fig. 4), and because there are no clear morphological synapomorphies for the expanded family concept.

Many generic concepts in Eupolypods II are in flux and although not a focus of our classification, we attempt to account for all generic names in current general usage, and provide a

familial placement. For each family, we provide: a list of defining morphological characters (from the references cited in the family header, from our direct observations, and from the following general references: Wilson, 1959; Ogura, 1972; Tryon & Tryon, 1982; Gifford & Foster, 1989), nomenclatural data, and a list of included genera and the estimated number of species. In addition, we recommend possible English family names, and summarize information on ecology, geographic range, and phylogenetic relationships. Each family is accompanied by a concept map (see Franz & al., 2008), mapping our treatment onto previous classifications. For example, the following entry under Rhachidosoraceae: “=Athyraceae: Rhachidosoroideae sensu Wang & al. (2004); <Woodsiaceae sensu Smith & al. (2006)” indicates that our treatment of that family is equivalent in composition to Wang & al.’s concept of subfamily Rhachidosoroideae of Athyraceae, and is a subset of Smith & al.’s concept of Woodsiaceae. Family names are based on those in Hoogland & Reveal (2005), except for Diplaziopsidaceae and Rhachidosoraceae, which are from Christenhusz & al. (2011), and Hemidictyaceae, from Christenhusz & Schneider (2011).

■ CYSTOPTERIDACEAE (Payer) Shmakov, *Turczaninowia* 4: 60 (2001)

Cystopteridoids; Bladderferns, Brittleferns, Oakferns, and allies. Approximately 30 species in the genera *Acystopteris* Nakai (3 spp.), *Cystoathyrium* Ching (1 sp.), *Cystopteris* Bernh. (~20 spp.; incl. *Rhizomatopteris* A.P. Khokhr.), and *Gymnocarpium* Newman (~7 spp.; incl. *Currantia* Copel.); (Tagawa, 1935; Blasdell, 1963; Vida, 1974; Sarvela, 1978; Haufler & Windham, 1991; Pryer & Haufler, 1993).

<Polypodiaceae: Asplenoideae+Polypodiaceae: Dryopteridoideae sensu Christensen (1938); <Dennstaedtiaceae: Dryopteridoideae+Athyraceae sensu Holttum (1947); <Dryopteridaceae: Dryopteridoideae+Athyraceae sensu Nayar (1970); <Athyraceae sensu Pichi Sermolli (1977); <Athyraceae sensu Ching (1978a); <Dryopteridaceae: Athyraceae sensu Lovis (1978); <Dryopteridaceae: Phymatiaeae sensu Tryon & Tryon (1982); <Dryopteridaceae: Athyraceae: Phymatiaeae sensu Kramer & al. (1990b); <Cystopteridaceae sensu Shmakov (2001); <Athyraceae: Cystopterioideae sensu Wang & al. (2004); <Woodsiaceae sensu Smith & al. (2006); =Cystopteridaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial; roots blackish, wiry, inserted radially, non-proliferous; rhizomes epigeous or more often subterranean, short- to more often long-creeping, occasionally suberect (*Cystopteris*), commonly branched, bearing scales and sometimes golden hairs similar to the root-hairs (e.g., *C. protrusa* (Weath.) Blasdell); rhizome scales lanceolate, clathrate or non-clathrate, the margins glandular or not, without distinct pubescence, entire to ciliate, the teeth when present not formed by two adjacent cells; leaves green and not covered in mucilage during any stage of development, spirally arranged, monomorphic, bulbiferous in a few *Cystopteris*, closely spaced to distant, bearing scales and sometimes gland-tipped hairs, the scales sometimes reduced to filiform proscapes (*Cystopteris*) or catenate hairs (*Acystopteris*); petioles stramineous throughout

or proximally darkened, the base narrow, or conspicuously thickened and then starch-filled and persistent (trophopods), without conspicuous aerophores, without a proximal articulation, sometimes with golden hairs similar to the root hairs (e.g., *C. moupinensis* Franch.); petiolar vascular bundles two, the bundles with hippocampiform-shaped xylem, distally uniting to form a single V-shaped bundle; laminae thin-herbaceous, 2–3-pinnate-pinnatifid (pinnate-pinnatifid in *Cystoathyrium*), broadest at the base or lanceolate, the apex non-conform, the leaf marginal cells differentiated into nodulose hyaline cells (*Acystopteris*, *Cystopteris*) or not (*Gymnocarpium*); pinna axes distinctly articulate in *Gymnocarpium*, otherwise non-articulate, sulcate adaxially, lacking a free central ridge; the rachis grooves continuous or not, the sulcus wall of the rachis continuing as a prominent ridge onto the sulcus wall of the costa or not; veins free, terminating at the leaf margin, the vein endings not differentiated; sori dorsal along veins, not terminal, round or slightly elongate (*Gymnocarpium*), indusiate (*Acystopteris*, *Cystoathyrium*, *Cystopteris*) or exindusiate (*Gymnocarpium*); soral receptacle distinctly raised and hardened (*Acystopteris*, *Cystopteris*) or flat (*Gymnocarpium*); indusia basal (*Acystopteris*, *Cystoathyrium*, *Cystopteris*); sporangia with stalks two or three cells wide in the middle; spores monoletate, non-chlorophyllous, tan (*Acystopteris*) or brown, the perispore echinate, tuberculate, or with broad folds, the folds sometimes perforate; chromosome base number $x = 40$ (*Gymnocarpium*; Kato & al., 1992; Pryer & Haufler, 1993) or 42 (*Acystopteris*, *Cystopteris*; Blasdell, 1963; Vida, 1974; Mitui, 1975). Reports of $x = 41$ (e.g., Christenhusz & al., 2011) are not substantiated.

Although the genera are distinctive, Cystopteridaceae as a whole are not easily characterized. Among families with petioles that contain two vascular bundles, they can be distinguished by an absent or hood-like indusium, usually long-creeping and subterranean rhizome, and veins that terminate at the leaf margin.

The indusia of *Acystopteris*, *Cystoathyrium*, and *Cystopteris* are unique in being attached at the base of the sporangia and curving, hood-like, around them. The sorus itself is situated upon a raised and hardened receptacle; we know of no other taxa within Eupolypods II with a similar receptacle. *Woodsia* also has a basally attached indusium, however, it can be distinguished by having a flat receptacle, the indusium encircling the sorus, usually dissected into multiple lobes, and veins that do not reach the leaf margin.

Gymnocarpium can be diagnosed by its articulate pinnae (that do not disarticulate) with a swollen protuberance at the base of each pinna. Among Eupolypods II, articulate pinnae also occur in *Stenochlaena* and *Woodwardia virginica* (L.) Sm. Those articulations differ, however, by lacking the basal protuberance present in *Gymnocarpium*. *Gymnocarpium* can also be distinguished from other Eupolypods II by having slightly elongate sori that lack an indusium. These sori are about twice as long as wide, and appear round until the sporangia are removed to reveal an elongate patch of sporangial stalks spreading along the vein.

Biology and phylogeny. — Cystopteridaceae are unusual in their primarily temperate distribution and tendency to occupy montane habitats. Both *Cystopteris* and *Gymnocarpium*

are common ferns of the north temperate zone, with *Cystopteris* also ranging south in montane habitats through the Andes and Himalayas, and to Australia, New Zealand, Hawaii, and southern Africa. Within the family, *Acystopteris* is the only genus found commonly in tropical areas; it is most rich in East Asia (Blasdell, 1963; Sarvela, 1978; Pryer, 1993).

The relationships of genera within Cystopteridaceae have been the subject of unusually strong disagreement; their affinities have been extremely difficult to infer from morphology, even more so than is typical for most eupolypod II taxa. Individually, both *Cystopteris* s.l. (i.e., including *Acystopteris*; Tagawa, 1935; Blasdell, 1963) and *Gymnocarpium* have been thought to be allied with Dryopteridaceae (in Eupolypods I) or Athyriaceae; in either position they were inevitably highlighted as being anomalous (see Sledge, 1973). Ching (1940) was an early exception, however, in placing both *Cystopteris* and *Gymnocarpium* together, but among the athyrioids.

Early molecular data supported *Cystopteris* and *Gymnocarpium* as sister genera (one accession each; *Acystopteris* was not sampled), and demonstrated their lack of close affinity to either Dryopteridaceae or *Athyrium*, but were unable to resolve their position within a broad assemblage of eupolypod II taxa (Wolf & al., 1994; Hasebe & al., 1995). In their landmark study, Sano & al. (2000a) included four representatives from this clade: one *Acystopteris*, one *Cystopteris*, and two *Gymnocarpium* species. Their within-clade relationships were consistent with earlier studies (*Acystopteris* + *Cystopteris* sister to *Gymnocarpium*), but they did not find support for the clade's placement within Eupolypods II. Conversely, Schuettpelz & Pryer (2007) in their broad study across ferns, included fewer taxa from this clade (a single *Gymnocarpium* and a single *Cystopteris*) but more character data; they were the first to find support for a sister-group relationship between this clade and the rest of Eupolypods II. Similarly, Kuo & al. (2011), using three plastid loci and single accessions of *Acystopteris* and *Gymnocarpium*, also recovered the sister-group relationship of this clade to the rest of Eupolypods II. The results of Rothfels & al. (2012) corroborate and strengthen that finding (Fig. 4).

Cystopteris and *Acystopteris* are strongly supported as sister, and are in turn sister to *Gymnocarpium*. The type species of all three genera have been included in molecular phylogenetic studies, as have those of the segregates *Rhizomatopteris* and *Currantia*: *Rhizomatopteris* is sister to the remaining species of *Cystopteris* s.str.; *Currantia* is embedded within *Gymnocarpium* (Sano & al., 2000a; Rothfels & al., 2012). Cystopteridaceae was first circumscribed by Shmakov (2001), who included *Pseudocystopteris* (which belongs in Athyriaceae) and omitted *Acystopteris* and *Cystoathyrium* (which were not in his geographic range).

The position of the monotypic genus *Cystoathyrium* is uncertain. In describing the genus, Ching (1966) emphasized its morphological intermediacy between *Cystopteris* and *Athyrium*, and little progress has since been made towards resolving its affinities. Wang & al. (2004, 2008) treated it as allied to *Cystopteris*, whereas Kramer & al. (1990b) place it in *Athyrium*, a position also advocated by Pichi Sermolli (1977). *Cystoathyrium* has yet to be included in any phylogenetic study, and we

know it only from photographs and the illustration provided in the protologue; it is possibly extinct (X.-C. Zhang, pers. comm.). Other genera historically thought to be allied with *Cystopteris* (most notably *Pseudocystopteris*; Ching, 1964a) have been shown to be nested within Athyriaceae (Sano & al., 2000a; Liu, 2008; Rothfels & al., 2012), however, we tentatively include *Cystoathyrium* here in Cystopteridaceae based on four characters: round sori, hood-like indusium, strongly echinate spores, and veins that terminate at the leaf margin. Although homoplastic within Eupolypods II, these character states occur most frequently in Cystopteridaceae. More research is needed; *Cystoathyrium* may be an isolated lineage within the Eupolypods II.

■ RHACHIDOSORACEAE X.C. Zhang, *Phytotaxa* 19: 16 (2011)

Lacquer Ferns. Four to seven species of the genus *Rhachidosorus* Ching; (Ching, 1964a; Kato, 1975a; Li & al., 2011).

<Polypodiaceae: Asplenoioideae sensu Christensen (1938); <Dennstaedtiaceae: Athyrioideae sensu Holttum (1947); <Dryopteridaceae: Athyrioideae sensu Nayar (1970); <Athyriaceae sensu Tagawa & Iwatsuki (1972); =“*Diplazium mesosorum* group” sensu Kato (1977); <Athyriaceae sensu Pichi Sermolli (1977); <Athyriaceae sensu Ching (1978a); <Dryopteridaceae: Athyrioideae sensu Lovis (1978); <Dryopteridaceae: Physematieae sensu Tryon & Tryon (1982); <Dryopteridaceae: Athyrioideae: Physematieae sensu Kramer & al. (1990b); =Athyriaceae: Rhachidosoroideae sensu Wang & al. (2004); <Woodsiaceae sensu Smith & al. (2006); =Rhachidosoraceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial; roots inserted radially, non-proliferous; rhizomes creeping or short-creeping, not commonly branched, bearing scales; rhizome scales lanceolate, clathrate, the margins entire, without distinct pubescence; leaves green and not covered in mucilage during any stage of development, spirally arranged, monomorphic, not articulate to the rhizome, closely spaced, sparsely scaly; petioles reddish to stramineous throughout, narrow at the base, not forming trophopods, without conspicuous aerophores, without a petiolar articulation; petiolar vascular bundles two, each with hippocampiform xylem, the bundles distally uniting to form a single U-shaped bundle; laminae herbaceous, 2–3-pinnate-pinnatifid, broadest at the base, the apex non-conform, the leaf marginal cells differentiated into nodulose hyaline cells; pinna axes not articulate, sulcate adaxially, lacking a free central ridge; the rachis grooves U-shaped, continuous, the sulcus wall of the rachis continuing as a prominent ridge onto the sulcus wall of the costa, and then departing on the costule of the first basiscopic segment; veins free, terminating before the leaf margin, the vein endings not differentiated; sori dorsal along veins, not terminal, elongate, indusiate; soral receptacle flat; indusia lateral, non-glandular; sporangia with stalks two or three cells wide in the middle; spores monolete, non-chlorophyllous, brown, the perispore echinate, tuberculate, or with broad folds, the folds sometimes perforate; chromosome base number $x = 41$ (Kato, 1975a; Kato & al., 1992; Takamiya & al., 2000). The count of $x = 40$ (Kurita, 1960) is unsubstantiated.

Rhachidosoraceae can be distinguished by the combination of subterranean creeping rhizomes, leaves without abundant anthocyanins or mucilage at any stage, petioles with two vascular bundles, elongate sori restricted to one side of the vein, with indusia, and laminae provided with narrow filiform scales, and lacking hairs. This suite of characters, however, renders it difficult to distinguish from either Aspleniaceae or Athyriaceae. With Aspleniaceae it shares clathrate scales and elongate sori that are largely confined to one side of the vein. It does not, however, have the pinna-costa architecture characteristic of Aspleniaceae—a non-sulcate petiole where wings are formed by a decurrent lamina margin. (See the key provided below for additional technical characters distinguishing Rhachidosoraceae from Aspleniaceae.) More difficult is distinguishing Rhachidosoraceae from Athyriaceae; both families have similar pinna-costa architecture. This architecture is characterized by a sulcate rachis that is not alate, and that has a prominent flange on the basisopic side of the pinna costa formed by the sulcus wall as it continues from the rachis onto the pinna costa itself. In addition, *Rhachidosorus* has minute corniculae and scales adaxially at the junction of the pinna and rachis, which are similar to those of *Athyrium* and *Cornopteris*. The most useful characters for distinguishing between these two families are the clathrate scales and linear sori confined to one side of the vein in Rhachidosoraceae; most Athyriaceae have sori on two sides of a single vein, either back-to-back, or in a hooked arrangement.

Biology and phylogeny. — Endemic to Asia, *Rhachidosorus* is a genus of approximately eight species of understory terrestrial ferns, which are often found in limestone habitats, and are very similar in gross morphology to species of *Athyrium*. Based on morphology, *Rhachidosorus* was previously included in either *Athyrium* (Makino, 1899) or *Diplazium* (Kato, 1975a), or considered a closely allied segregate (Ching, 1964a; reviewed in Sano & al., 2000a). Early molecular phylogenies (Sano & al., 2000a; Tzeng, 2002; Wang & al., 2003), however, unexpectedly suggested that *Rhachidosorus* was not closely related to either *Athyrium* or *Diplazium*. These results were later corroborated by the three-gene study of Kuo & al. (2011) who resolved *Rhachidosorus* as sister to the large clade of Thelypteridaceae + *Woodsia* + Athyriaceae + Blechnaceae + Onocleaceae, but with only weak support, and by Li & al. (2011) who placed the genus as sister to the clade recognized here as Diplaziopsidaceae. These studies each included a single *Rhachidosorus* accession (*R. mesosorus* (Makino) Ching in Sano & al., 2000a; *R. consimilis* Ching in Wang & al., 2003; *R. pulcher* (Tagawa) Ching in Tzeng, 2002 and Kuo & al., 2011), except for Li & al. (2011) who included both *R. consimilis* and *R. blotianus* Ching. The five-locus dataset of Rothfels & al. (2012) also included two species (*R. mesosorus*, *R. pulcher*), but as with the other studies was unable to strongly support the phylogenetic position of the genus; it was weakly placed as sister to Diplaziopsidaceae + Hemidictyaceae + Aspleniaceae.

Molecular data from four species (including *R. mesosorus*, the type of the genus) and six independent studies consistently support the surprising finding that *Rhachidosorus* is not phylogenetically close to *Athyrium* or *Diplazium*, but instead comprises an isolated lineage within Eupolypods II. The phylogeny

of Rothfels & al. (2012) suggests that *Rhachidosorus* diverged from its nearest relatives approximately 90 million years ago, long before, for example, the ancestors of *Blechnum* diverged from those of *Athyrium* (Fig. 4) (Rothfels & al., 2012, their Supplementary Fig. 1).

■ DIPLAZIOPSIDACEAE X.C. Zhang & Christenh., *Phytotaxa* 19: 15 (2011)

Glade Ferns. Approximately four to six species of the genera *Diplaziopsis* C. Chr. (2–4 spp.), *Homalosorus* Pic. Serm. (1 sp.), plus *Diplazium flavoviride* Alston; (Ching, 1964b; Kato, 1975b; Kato & Darnaedi, 1988; Wei & al., 2010; Li & al., 2011).

<Dennstaedtiaceae: Athyrioideae sensu Holttum (1947); <Dryopteridaceae: Athyrioideae sensu Nayar (1970); <Athyriaceae sensu Tagawa & Iwatsuki (1972); <“*Diplazium javanicum* group” sensu Kato (1977); <Athyriaceae sensu Pichi Sermolli (1977); <Athyriaceae sensu Ching (1978a); <Dryopteridaceae: Athyrioideae sensu Lovis (1978); <Dryopteridaceae: Phymatiae sensu Tryon & Tryon (1982); <Dryopteridaceae: Athyrioideae: Phymatiae sensu Kramer & al. (1990b); <Athyriaceae: Diplazioidae sensu Wang & al. (2004); <Woodsiaceae sensu Smith & al. (2006); <Diplaziopsidaceae + Athyriaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial or epipetric; roots fleshy, pale, inserted radially, non-proliferous; rhizomes erect to suberect (*Diplaziopsis*, *Diplazium flavoviride*) or short-creeping (*Homalosorus*), commonly unbranched, bearing scales, and sometimes golden hairs similar to the root hairs (*Homalosorus*); rhizome scales lanceolate, non-clathrate, the margins entire, non-glandular, without distinct pubescence; leaves green and not covered in mucilage during any stage of development, spirally arranged, monomorphic, non-bulbiferous, closely spaced, glabrous (*Diplaziopsis*) or with filiform proscas (*Homalosorus*); petioles stramineous throughout or proximally darkened, thin, without a proximal thickening, conspicuous aerophores, or proximal articulation, sometimes with golden hairs similar to the root hairs (*Homalosorus*); petiolar vascular bundles two, each with hippocampiform xylem, the bundles distally uniting to form a single V-shaped bundle; laminae soft-herbaceous, 1-pinnate, the apex conform (*Diplaziopsis*) or non-conform (*Homalosorus*), the leaf marginal cells differentiated into nodulose hyaline cells; pinna axes not articulate, sulcate adaxially, lacking a free central ridge; the rachis grooves V-shaped, not continuous, the sulcus wall of the rachis continuing as a prominent ridge onto the sulcus wall of the costa; veins free (*D. flavoviride*, *Homalosorus*) or anastomosing toward the pinna margins (*Diplaziopsis*), the areoles without free included veinlets, usually terminating before the leaf margin, however some veins reaching the leaf margin in *D. flavoviride* and *Homalosorus*, the vein endings differentiated, slightly raised and expanded; sori singular along one side of the vein, rarely paired back to back along the same vein, elongate, indusiate, not terminal; soral receptacle flat; indusia lateral, vaulted or essentially flat, glabrous or glandular (*Diplaziopsis*), opening along the lateral margin or sometimes rupturing irregularly (*Diplaziopsis*); sporangia with stalks two or three cells wide in the middle; spores monolet, non-chlorophyllous, brown, the

perispore folded with thin crests, the crests erose; chromosome base numbers $x = 40$ (*Diplazium flavoviride*, *Homalosorus*; Löve & al., 1977; Kato & Darnaedi, 1988) or 41 (*Diplaziopsis*; Mitui, 1975; Takamiya & Ohta, 2001).

Diplaziopsidaceae can be recognized by the combination of petioles with two vascular bundles, 1-pinnate laminae, elongate sori that are usually along one side of the vein only, vein endings that are thickened and raised adaxially, and by the sulcus wall of the rachis forming a ridge that connects to the pinna sulcus wall of the pinna costa. The thickened and raised vein endings are a particularly useful diagnostic character among Eupolypods II, because they are otherwise only found in *Hemidictyum* (Hemidictyaceae). *Hemidictyum* also has a 1-pinnate lamina, a conform terminal segment, and veins that anastomose towards the pinna margins, similar to *Diplaziopsis*; however, it differs in several other respects, most conspicuously by having a sub-marginal collecting vein, and pinna margins that have a broad, pale membranaceous edge.

As Price (1990) noted, leaves of Diplaziopsidaceae are conspicuously soft, green, and fleshy. The pale fleshy roots appear to be unique among Eupolypods II, and anatomical study may provide synapomorphies for the family. However, the claim by Price (1990) that the plants entirely lack sclerenchyma is overstated; sclerenchyma occurs in the cortex and xylem, as evidenced by staining with toluidine blue (Sundue & Rothfels, unpub. data). Diplaziopsidaceae are most likely to be confused with Athyriaceae, particularly *Diplazium*, which is morphologically similar. Diplaziopsidaceae differs from most *Diplazium* species, however, by the usually singular linear sori, non-continuous groove of the adaxial pinnae-costa junctions, the near absence of indument on the lamina, the narrow petiole bases that do not form trophopods, thickened vein endings, and vaulted indusium, when it is present.

Biology and phylogeny. — Diplaziopsidaceae are medium-sized ferns of mesic understory habitats. They show an interesting pattern of disjunction, with the monotypic *Homalosorus* being a common member of rich temperate forests of eastern North America, while the *Diplaziopsis* species and *Diplazium flavoviride* are found in Asia, extending east to the Pacific islands (Kato & Darnaedi, 1988).

The history of typification of *Diplaziopsis* is convoluted. Christensen (1906: XXXII) published it as a replacement name for *Allantodia* Wall., 1830 (a later homonym of *Allantodia* R. Br., 1810). As a replacement name, therefore, *Diplaziopsis* takes the type of *Allantodia* Wall., which is *A. brunoniana* Wall. However, Christensen did not publish a combination for *A. brunoniana* under *Diplaziopsis* (he considered *A. brunoniana* to be a synonym of *Asplenium javanicum* Blume); the combination *Diplaziopsis brunoniana* (Wall.) W.M. Chu was made only recently (Chu & Zhou, 1994). Christensen (1906) listed *Asplenium javanicum* (= *Diplaziopsis javanica* (Blume) C. Chr.) as the type of *Diplaziopsis*, but this is prohibited under Art. 7.3 of the *Vienna Code*. However, if *Diplaziopsis brunoniana* is regarded as a heterotypic synonym of *D. javanica*, as Christensen (1906: CCXXVII) indicated, then *D. javanica* has priority and must be used as the name of the species, and the type of the genus. Alternatively, if *D. brunoniana* and *D. javanica* are

recognized as distinct (as by Chu & He, 1999), then the type of the genus remains *D. brunoniana*.

Prior to the availability of molecular data, members of this clade were consistently thought to belong with the athyrioids, and both *Diplaziopsis* and *Homalosorus* were typically treated as members of *Diplazium* (Ching, 1964b; Kato, 1975b, 1977, 1993; Kato & Darnaedi, 1988; Wang & al., 2004). The first indication that this placement might be inaccurate came from the study of Sano & al. (2000a), in which the monotypic *Homalosorus* was strongly supported as sister to *Diplaziopsis cavalieriana* (Christ.) C. Chr., with these two taxa forming an isolated lineage distant from *Diplazium*. The next molecular phylogenetic study to include members of this clade was by Wei & al. (2010), and their results placed the two genera together in an unresolved position within the Eupolypods. Kuo & al. (2011), with more character data and denser taxon sampling, again resolved *Diplaziopsis* as sister to *Homalosorus*. Their results showed that this combined lineage—*Diplaziopsis*+*Homalosorus*—diverged from the rest of the Eupolypods II at an unsupported position deep along the eupolypod II backbone. The results of Li & al. (2011) were similar (*Diplaziopsis* sister to *Homalosorus*, and that clade distant from *Diplazium*), with the exception that their study placed the *Diplaziopsis*+*Homalosorus* clade as sister to *Rhachidosorus*.

In the analyses of Rothfels & al. (2012), *Diplaziopsis cavalieriana* and *D. javanica* are strongly supported as sister, and together they are sister to *Homalosorus*. These data allow either for the recognition of a monotypic *Homalosorus*, or its treatment within *Diplaziopsis*, as *D. pycnocarpa* (Spreng.) M.G. Price (Price, 1990). Diplaziopsidaceae diverged from Hemidictyaceae+Aspleniaceae early in the diversification of Eupolypods II—these two lineages shared a most recent common ancestor some 90 million years ago (Fig. 4) (Rothfels & al., 2012, their Supplementary Fig. 1)—further supporting the recognition of Diplaziopsidaceae rather than merging it into an expanded Aspleniaceae. *Diplazium flavoviride* has not been included in any phylogenetic analyses, but is included here based on the arguments of Kato & Darnaedi (1988). *Hemidictyum*, however, does not fall in Diplaziopsidaceae; its inclusion in that family by Christenhusz & al. (2011) rendered their concept of Diplaziopsidaceae paraphyletic, an error they subsequently corrected (Christenhusz & Schneider, 2011).

■ HEMIDICTYACEAE Christenh. & H. Schneid., *Phytotaxa* 28: 51 (2011)

Hemidictyum. One species of the genus *Hemidictyum* C. Presl.; (Kato, 1975b).

<Dennstaedtiaceae: Athyrioideae sensu Holttum (1947); <Dryopteridaceae: Athyrioideae sensu Nayar (1970); <“*Diplazium javanicum* group” sensu Kato (1977); <Athyriaceae sensu Pichi Sermolli (1977); <Thelypteridaceae sensu Lovis (1978); <Dryopteridaceae: Phytosmatieae sensu Tryon & Tryon (1982); <Dryopteridaceae: Athyrioideae: Phytosmatieae sensu Kramer & al. (1990b); <Woodsiaceae sensu Smith & al. (2006); <Diplaziopsidaceae sensu Christenhusz & al. (2011); =Hemidictyaceae sensu Christenhusz & Schneider (2011).

Characters. — Plants terrestrial; roots inserted radially, proliferous; rhizomes erect or suberect, commonly unbranched, bearing scales; rhizome scales lanceolate, weakly-clathrate, the margins entire, non-glandular, without distinct pubescence; leaves green and not covered in mucilage during any stage of development, spirally arranged, monomorphic, non-bulbiferous, closely spaced, glabrous; petioles stramineous throughout or proximally darkened, thin, not forming trophopods, lacking conspicuous aerophores, without a petiolar articulation; petiolar vascular bundles two, each with hippocampiform xylem, the bundles distally uniting to form a single U-shaped bundle; laminae herbaceous, 1-pinnate, the apex conform, the lateral pinnae sub-opposite, the pinna bases cordate, the leaf margin differentiated into a broad membranaceous edge; pinna axes not articulate, sulcate adaxially, lacking a free central ridge; the rachis grooves not continuous, the sulcus wall of the rachis not continuing as a ridge along the costa; veins anastomosing toward the pinna margins, the areoles without free included veinlets, terminating before the leaf margin and forming a sub-marginal collecting vein, the vein endings differentiated, slightly raised and expanded; sori usually singular along one side of the vein, occasionally back-to-back along both sides of the vein, elongate, indusiate, not terminal; soral receptacle flat; indusia lateral, essentially flat, glabrous; sporangia with stalks two or three cells wide in the middle; spores monolete, non-chlorophyllous, brown, the perispore with broad folds and tubercles, the folds sometimes perforate; chromosome base number $x = 31$ (Walker, 1973a; F.S. Wagner, 1980).

Although its conform apical pinnae, pattern of anastomosing veins, and thickened and raised vein endings are shared with *Diplaziopsis*, Hemidictyaceae can be distinguished from all other Eupolypods II by the combination of its sub-marginal collecting vein and pinna margin that is differentiated into a broad membranaceous border. Hemidictyaceae are sister to Aspleniaceae, but the two families together share no known synapomorphies. One character that should be investigated further is whether roots are proliferous, yielding new plants asexually. Walker (1985: 217) reported such roots in *H. marginatum* (L.) C. Presl.; they also occur in some species of *Asplenium* (Mickel & Smith, 2004), although sporadically enough that a synapomorphy for the two families is unlikely.

Biology and phylogeny. — *Hemidictyum* is a monotypic genus of the New World tropics—from southern Mexico to southeastern Brazil—where it grows at low to mid elevations in wet forests. The genus has always been an awkward fit in fern classifications, with opinions alternating for an alliance with thelypteroid ferns (based on spore morphology, e.g., Lovis, 1978), *Diplaziopsis* (based on its sagenoid venation, e.g., Kato, 1975b), or with Dryopteridaceae (in Eupolypods I; e.g., Tryon & Tryon, 1982).

Kato's (1975b) study was the first to emphasize commonalities between *Hemidictyum* and *Diplaziopsis*, and he argued that they might be isolated from much of *Diplazium* (Kato, 1975b). Molecular data (Schuettpelz & Pryer, 2007; Kuo & al., 2011; Rothfels & al., 2012) corroborated this morphology-based hypothesis, in part; *Hemidictyum* (like *Diplaziopsis*) is not

closely related to *Diplazium* s.str.—*Hemidictyum* and *Diplaziopsis* + *Homalosorus* are more closely related to each other than to any eupolypod II lineage outside of Aspleniaceae.

Given its sister relationship with *Asplenium* + *Hymenasplenium*, *Hemidictyum* could be subsumed within an expanded concept of Aspleniaceae while retaining the monophyly of the latter family (Fig. 4). However, we favor recognizing Hemidictyaceae, even though it is monotypic, because the most recent common ancestor of *Hemidictyum* and Aspleniaceae dates to the Late Cretaceous (approximately 85 million years ago, Fig. 4) (Rothfels & al., 2012, their Supplementary Fig. 1), *Hemidictyum* would be morphologically anomalous within Aspleniaceae, and Aspleniaceae has a long history of taxonomic treatment excluding *Hemidictyum*.

■ ASPLENIACEAE Newman, Hist. Brit. Ferns: 6 (1840)

Spleenworts. Approximately 700 species of one to ten genera, dominated by the large genus *Asplenium* L. (incl. *Antigramma* C. Presl., *Asplenidictyum* J. Sm. in Hook., *Biropteris* Kümmerle, *Camptosorus* Link, *Ceterach* Willd., *Diellia* Brack. in Wilkes, *Diplora* Baker, *Holodictyum* Maxon, *Loxoscapha* T. Moore, *Neottopteris* J. Sm., *Phyllitis* Hill, *Pleurosorus* Fée, *Schaffneria* Fée, *Scolopendrium* Adans., and *Sinephropteris* Mickel) and with a small genus *Hymenasplenium* Hayata (incl. *Boniniella* Hayata); (Murakami, 1995; Murakami & al., 1999; Gastony & Johnson, 2001; Schneider & al., 2004a).

<Polypodiaceae: Asplenioidae sensu Christensen (1938); =Dennstaedtiaceae: Asplenioidae sensu Holttum (1947); =Aspleniaceae sensu Nayar (1970); =Aspleniaceae sensu Tagawa & Iwatsuki (1972); =Aspleniaceae sensu Pichi Sermolli (1977); =Aspleniaceae sensu Lovis (1978); =Aspleniaceae sensu Tryon & Tryon (1982); =Aspleniaceae sensu Kramer & Viane (1990); =Aspleniaceae sensu Smith & al. (2006); =Aspleniaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial, epipetric, or epiphytic, sometimes rheophytic; roots blackish, wiry, inserted radially or ventrally (*Hymenasplenium*), proliferous or non-proliferous; rhizomes usually odorless, rarely with the odor of wintergreen (e.g., *A. longissimum* Blume), short- to long-creeping, or suberect, branched or more commonly unbranched, sometimes massive and forming a detritus-collecting basket (e.g., *A. nidus* L.), bearing scales; rhizome scales lanceolate, clathrate, usually with blackish cell walls and hyaline lumens, sometimes brown or golden-brown, the margins glandular or not, entire to dentate or ciliate, without distinct pubescence; leaves green and not covered in mucilage during any stage of development, usually monomorphic, sometimes hemi-dimorphic, spirally arranged or distichous and dorsal (*Hymenasplenium*), occasionally bulbiferous, the bulbils frequently at the leaf apex, in a distal pinna axil, or at the base of the lamina, leaves usually closely spaced, sparsely to densely scaly, occasionally pubescent, rarely glandular (e.g., *A. platyneuron* (L.) Britton, Sterns & Poggenb.), also frequently with minute filiform proscapes; petioles dull and greenish, gray, or

brownish, or lustrous and castaneous, atropurpureous, or ebenous, the bases expanded in *Hymenasplenium*, otherwise not usually expanded, persistent or not, articulate to the rhizome in *Hymenasplenium*, otherwise not; petiolar vascular bundles two, each with C-shaped xylem, the bundles distally uniting to form a single X-shaped bundle; laminae soft-herbaceous to coriaceous, simple to 4-pinnate, the apex usually pinnatifid or non-conform, occasionally conform (e.g., *Asplenium davisii* Stolze), the leaf marginal cells usually not differentiated; pinna axes not articulate, among species with divided leaves the axes usually alate, with wings derived from a decurrent and thickened leaf margin, or the wings thin, fragile, and apparently derived from the rachis; the rachis axes usually not sulcate adaxially, without a free central ridge; veins free or anastomosing, the areoles without free included veinlets, reaching the leaf margin or terminating before it, some species with a sub-marginal collecting vein, the vein endings forming hydathodes, or not differentiated; sori elongate, along one side of the vein, rarely paired back to back, and then usually not along the same vein, and if so then usually where groups of veins converge, indusiate; soral receptacle flat; indusia lateral, essentially flat, glabrous or sometimes glandular, opening along the lateral margin; sporangia with stalks one cell wide in the middle; spores monoletate, non-chlorophyllous, brown, the perispore with sharp ridges or broad folds, sometimes echinulate, fenestrate, or reticulate; chromosome base numbers $x = 36$ (most species, e.g., Bir & Shukla, 1967; Walker, 1973a; Smith & Mickel, 1977), 38 (*Hymenasplenium*; Murakami, 1995), and 39 (*Hymenasplenium*; Kato & al., 1990; Murakami, 1995).

Aspleniaceae exhibit a broad spectrum of morphological diversity, yet identification of the family is usually not difficult. Diagnostic for Aspleniaceae are the linear sori with lateral indusia restricted to one side of the vein. The so-called “back-to-back” or “diplazioid” sori occur in some Aspleniaceae, however, they tend to be restricted to small portions of the lamina. As Holttum (1954) pointed out, patterns of major vein groups suggest that these instances are likely the result of lamina fusion or reduction. Some species of *Hymenasplenium* have been confused with *Diplazium* (Smith, 1976). However, numerous technical apomorphies of Aspleniaceae serve to distinguish these two genera. See the first lead in the key to families provided below for a list of characters serving to separate Aspleniaceae from other eupolypod II families.

Biology and phylogeny. — Aspleniaceae are a distinctive element within Eupolypods II; the family has usually been regarded as readily definable, in its current circumscription, even before Eupolypods II or Polypodiales (sensu Smith & al., 2006; Pryer & al., 2008) were recognized as cohesive entities (e.g., Nayar, 1970). Aspleniaceae are somewhat unusual considering their species-richness, in that they show strong patterns of diversification in both temperate and tropical areas (rather than being predominantly tropical), and have approximately equal numbers of epiphytic and terrestrial species (Schneider & al., 2004a). These two major habit types—epiphytic versus terrestrial—are both scattered across the Aspleniaceae phylogeny, although there is some evidence that the most recent common ancestor of the Aspleniaceae crown clade was epiphytic

(Schneider & al., 2004a). Our circumscription is identical to that of Smith & al. (2006), who include further information on this family.

■ THELYPTERIDACEAE Ching ex Pic. Serm., *Webbia* 24: 709 (1970)

Thelypteroids; Marsh Ferns, Beech Ferns, and allies. Approximately 950 species, divided among *Cyclosorus* Link (incl. *Amblovenatum* J.P. Roux, *Ampelopteris* Kunze, *Amphineuron* Holttum nom. illeg., *Chingia* Holttum, *Christella* H. Lév., *Christella* sect. *Pelazoneuron* Holttum, *Cyclogramma* Tagawa, *Cyclosorus* s.str., *Glaphyopteridopsis* Ching, *Goniopteris* C. Presl., *Meniscium* Schreb., *Mensorus* Alston, *Mesophlebion* Holttum, *Mesopteris* Ching, *Plesioneuron* (Holttum) Holttum, *Pneumatopteris* Nakai, *Pronephrium* C. Presl., *Pseudocyclosorus* Ching, *Sphaerostephanos* J. Sm., *Stegogramma* Blume, *Steiropteris* C. Chr., *Trigonospora* Holttum), *Macrothelypteris* (H. Ito) Ching, *Phegopteris* (C. Presl.) Fée, *Pseudophegopteris* Ching, and *Thelypteris* Schmidel (incl. *Amauropelta* Kunze, *Coryphopteris* Holttum, *Metathelypteris* (H. Ito) Ching, *Oreopteris* Holub, *Parathelypteris* (H. Ito) Ching, *Thelypteris* s.str., and *Wagneriopteris* Á. Löve & D. Löve); (Holttum, 1947, 1971c, 1981; Smith, 1990; Smith & Cranfill, 2002).

<Polypodiaceae: Dryopteridoideae sensu Christensen (1938); =Thelypteridaceae sensu Holttum (1947); =Thelypteridaceae sensu Nayar (1970); =Thelypteridaceae sensu Tagawa & Iwatsuki (1972); =Thelypteridaceae sensu Pichi Sermolli (1977); =Thelypteridaceae sensu Ching (1978a); <Thelypteridaceae sensu Lovis (1978); =Thelypteridaceae sensu Tryon & Tryon (1982); =Thelypteridaceae sensu Smith (1990); =Thelypteridaceae sensu Smith & al. (2006); =Thelypteridaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial, sometimes epipetric or rheophytic, rarely scandent (*Thelypteris* subg. *Amauropelta* sect. *Lepidoneuron* A.R. Sm.); roots blackish, wiry, inserted radially, non-proliferous; rhizomes not usually branched, short-to long-creeping, suberect, or erect, rarely sub-arborescent, bearing scales; rhizome scales lanceolate, non-clathrate, grayish to tan or brown, entire or dentate, the margins and often the surfaces usually bearing distinct pubescence similar to that of the leaves; leaves usually greenish in all stages, occasionally reddish when young (e.g., some *Cyclosorus* species treated in *Mesophlebion* and *Pronephrium*, possibly others), sometimes covered in mucilage when young, usually monomorphic, sometimes sub-dimorphic, spirally arranged, closely to distantly spaced, occasionally bulbiferous, the bulbils usually distal or apical on the leaf, scaly or not, almost always pubescent, the hairs whitish or hyaline, acicular, or sometimes forked, stellate, stalked-stellate, or hamate, also often provided with sessile or stalked glands; petioles greenish to stramineous, sometimes darker, the bases not articulate to the rhizome, not expanded at the base, and generally not persistent on the rhizome; petiole with two vascular bundles (rarely more), the bundles with hippocampiform-shaped xylem, distally uniting to form a single U-shaped bundle; laminae thin-herbaceous to coriaceous,

simple and entire to 3-pinnate-pinnatifid, in divided leaves, the base with or without a series of reduced pinnae, the apex conform or non-conform, the leaf marginal cells not clearly differentiated; pinna axes not articulate, the pinna base often with a conspicuous aerophore, these usually appearing as a low elongate or orbicular protuberance, or erect and vermiform, up to ca. 1 cm long; the rachis axes sulcate adaxially or not, when present the sulcae not continuous onto the next order, lacking a free central ridge; veins reaching the leaf margin or terminating before it, free, connivent at or below the sinus in lobed pinnae, or anastomosing in various patterns, the areoles without free included veinlets, the vein endings expanded or not differentiated; sori circular or elongate, on top of veins, not terminal, indusiate or exindusiate; soral receptacle flat; indusia lateral, reniform, sometimes pubescent and or glandular; sporangia with stalks more than one cell wide in the middle, often bearing hairs or glands (paraphysate); spores usually monolet, sometimes trilete (*Cyclosorus* treated as *Trigonospora*), non-chlorophyllous, the perispore brown, often with sharp crests, or reticulate or echinate; chromosome base numbers $x = 27$ (e.g., *Parathelypteris*; Weng & Qiu, 1988), 29 (e.g., *Amauropelta*; Walker, 1985), 30 (e.g., *Phegopteris*; Mitui, 1975), 31 (e.g., *Lastrea*, *Macrothelypteris*, *Pseudophegopteris*, *Wagneriopteris*; Mitui, 1975; Loyal, 1991; Tindale & Roy, 2002), 34 (e.g., *Oreopteris*; Holttum, 1981; Manton, 1950), 35 (e.g., *Metathelypteris*, *Pseudocyclosorus*, *Thelypteris*; Mitui, 1975; Loyal, 1991; Walker, 1985), or 36 (e.g., *Abacopteris*, *Ampelopteris*, *Amphineuron*, *Christella*, *Cyclogramma*, *Cyclosorus*, *Dictyocline*, *Goniopteris*, *Lastrea*, *Leptogramma*, *Meniscium*, *Pro-nephrium*, *Stenogramma*; Mitui, 1975; Walker, 1985; Loyal, 1991; Tindale & Roy, 2002).

Thelypteridaceae are a large and diverse family, however, they can usually be recognized by the presence of distinctive acicular hairs. These hairs are whitish or hyaline, and usually 1-celled. In addition to being on the leaves, these hairs also regularly occur upon the margins and faces of the rhizome scales. While dentate or ciliate scales are common, as far as we know, no other family in Eupolypods II has rhizome scales that bear hairs similar to those found upon the leaves. Hamate, forked, and stellate hairs also occur in Thelypteridaceae, which being uncommon in Eupolypods, are also useful diagnostic characters. Thelypteridaceae also frequently have conspicuous aerophores at the bases of their pinnae. These often differ in color and texture from the surrounding tissue, and are frequently raised. In some cases, elongate vermiform aerophores are present; these frequently occur in species in which the crosiers and young leaves are surrounded by thick mucilage.

Biology and phylogeny. — This large family is morphologically cohesive and has been long recognized as such, in its current circumscription (but cf. Hennipman, 1996). Within Thelypteridaceae, however, generic classifications vary widely, and only two molecular phylogenetic studies have included a substantial representation of the family (approximately 30 species each; Smith & Cranfill, 2002; Schuettpelz & Pryer, 2007). Our circumscription is identical to that of Smith & al. (2006), who discuss this family in further detail.

■ WOODSIACEAE Herter, *Revista Sudamer. Bot.* 9:14 (1949)

Woodsias; Cliff Ferns. Approximately 35 species of the genus *Woodsia* R. Br. (incl. *Cheilanthesis* Hieron., *Hymenocystis* C.A. Mey., and *Protowoodsia* Ching); (Brown, 1964; Kurita, 1965; Shmakov, 2003).

<Polypodiaceae: Woodsieae: Woodsiinae sensu Diels in Engler & Prantl (1897); <Polypodiaceae: Gymnogrammeoideae+Polypodiaceae: Woodsioideae sensu Christensen (1938); <Sinopteridaceae+Woodsiaceae sensu Ching (1940); <Dennstaedtiaceae: Dryopteridoideae sensu Holttum (1947); =Woodsiaceae sensu Herter (1949); <Dryopteridaceae: Dryopteridoideae sensu Nayar (1970); <Athriaceae sensu Tagawa & Iwatsuki (1972); =Woodsiaceae sensu Pichi Sermolli (1977); =Woodsiaceae sensu Ching (1978a); <Dryopteridaceae: Athyrioideae sensu Lovis (1978); <Dryopteridaceae: Physematieae sensu Tryon & Tryon (1982); <Dryopteridaceae: Athyrioideae: Physematieae sensu Kramer & al. (1990b); =Woodsiaceae sensu Wu & Ching (1991); <Woodsiaceae sensu Smith & al. (2006); =Woodsiaceae sensu Christenhusz & al. (2011).

Characters. — Plants epipetric, or occasionally terrestrial; roots blackish, wiry, inserted radially, non-proliferous; rhizomes short-creeping, horizontal to suberect, commonly unbranched, bearing scales; rhizome scales lanceolate, non-clathrate, the margins glandular or eglandular, without distinct pubescence, entire to denticulate or ciliate, the teeth when present formed by two adjacent cells, or not; leaves green and not covered in mucilage during any stage of development, usually spirally arranged, monomorphic, closely spaced, bearing scales and hairs, the hairs catenate or terete, sometimes gland-tipped (e.g., *W. mollis* (Kaulf.) J. Sm.), sometimes the scales forming a reduction series that terminates in broad-based, catenate, hair-like scales (e.g., *W. mollis*); petioles stramineous, castaneous or dark purple throughout, or proximally darkened, the base thin, not forming trochopods, persistent, usually forming a thick mantle of old petiole bases, without conspicuous aerophores, in some species with a petiolar articulation, the articulation usually proximal (e.g., *W. ilvensis* (L.) R. Br.) or just below the lamina; petiolar vascular bundles two, the bundles with hippocampiform-shaped xylem, distally uniting to form a single U-shaped bundle; laminae herbaceous, 1-pinnate to 2-pinnate-pinnatifid, usually broadest in the middle, the base with a series of reduced pinnae or not, the apex non-conform, the leaf marginal cells differentiated into nodulose hyaline cells or not; pinna axes not articulate, sessile or slightly petiolate; the rachis axes sulcate adaxially, lacking a free central ridge, the grooves not continuous; veins free, terminating before the leaf margin, the vein endings usually expanded and forming hydathodes; sori dorsal along veins, sub-terminal, or terminal (e.g., *W. elongata* Hook.), round, indusiate; soral receptacle distinctly flat; indusia basal, composed of a series of scale-like or filamentous segments or sometimes sac-like globose, glandular, pubescent, or not; sporangia with stalks two or three cells wide in the middle; spores monolet, non-chlorophyllous, tan or brown, the perispore echinate, tuberculate, or with broad folds or narrow crests, these sometimes forming a reticulum; chromosome base numbers $x = 33$ (*W. manchuriensis* Hook.; Kurita, 1965), 38, 39, or 41 (Manton, 1950; Brown, 1964).

When fertile, Woodsiaceae are easily diagnosed by the unique basal indusium composed of multiple scale-like or filamentous segments (occasionally as a single globose structure enclosing the sorus), which is unique among ferns. Many Cyatheaceae (in Cyatheales; see Fig. 1) have basal scale-like indusia, but these are generally more robust, are often spherical or cup-shaped, and do not consist of multiple segments. Some other taxa in Cyatheaceae have sori protected by scaly indument (e.g., *Sphaeropteris* subsect. *Fourniera* (J. Bommer ex Fourn.) P.G. Windisch); in these cases the scales resemble those of the lamina whereas in *Woodsia* they do not. Sterile leaves of Woodsiaceae, however, are not as easily characterized. When present, the petiolar articulation is a powerful diagnostic character, because it is unique in Eupolypods II, and rare outside of this clade. However, its utility is hindered by its absence from most species. Nonetheless, all species tend to accumulate large mats of persistent petiole bases, which are characteristic. In addition, the combination of 1-pinnate to 2-pinnate-pinnatifid leaves with sessile or short-petioled pinnae, laminae usually bearing scales and hairs (that are not acicular), and veins that terminate before the leaf margin in hydathodes serve to diagnose Woodsiaceae. Sterile plants of *Cystopteris* can appear surprisingly similar to those of *Woodsia*, however, they can be distinguished by having veins that reach the leaf margin.

Biology and phylogeny. — As circumscribed here, species of Woodsiaceae typically occur in rocky, montane areas, predominantly in the Northern Hemisphere. Areas of particular species-richness include the mountains of Eurasia, and arid areas of Mexico and southwestern U.S.A.; one polymorphic species (*W. montevidensis* (Spreng.) Hieron.) extends south through the Andes and also occurs in South Africa. They have remarkable ecological and morphological resemblance to members of *Cystopteris* (in Cystopteridaceae), to which they are only distantly related (Figs. 2, 4).

This family—comprising *Woodsia* and its segregates—is an isolated lineage, not closely related to the other taxa frequently included in broad concepts of Woodsiaceae (e.g., Smith & al., 2006). *Protowoodsia* and *Cheilanthesis* are nested within *Woodsia* s.l. (Rothfels & al., 2012), as is *Hymenocystis*, the other segregate genus recognized by Shmakov (2003; A. Larson, unpub.). The molecular phylogeny of *Woodsia* is marked by a remarkably deep split between a clade of Old World or holarctic species, and a clade of predominantly New World species. This deep dichotomy essentially mirrors the results of Brown's (1964) groundplan divergence scheme (W.H. Wagner, 1980) based upon morphological characters.

■ ATHYRIACEAE Alston, *Taxon* 5: 25 (1956)

Athyrioids; Ladyferns, and allies. Approximately 600 species, in *Anisocampium* C. Presl. (4 spp.; incl. *Kuniwatsukia* Pic. Serm.), *Athyrium* Roth (~220 spp.; incl. *Pseudocystopteris* Ching), *Cornopteris* Nakai (9 spp.; incl. *Neoathyrium* Ching & Z.R. Wang), *Deparia* Hook. & Grev. (~70 spp.; incl. *Athyriopsis* Ching, *Lunathyrium* Koidz., *Dictyodroma* Ching, *Dryoathyrium* Ching, and *Triblemma* R. Br. ex C. Sprengel),

and *Diplazium* Sw. (~300–400 spp.; incl. *Allantodia* R. Br., *Anisogonium* C. Presl., *Callipteris* Bory, *Monomelangium* Hayata; excl. *Diplazium flavoviride* Alston); (Kato, 1979, 1984; Tryon & Tryon, 1982; Pacheco & Moran, 1999; Sano & al., 2000b; Adjie & al., 2008; Liu, 2008; Liu & al., 2011).

<Polypodiaceae: Asplenioidae sensu Christensen (1938); <Dennstaedtiaceae: Athyrioideae sensu Holttum (1947); <Athyriaceae sensu Alston (1956); <Dryopteridaceae: Athyrioideae sensu Nayar (1970); <Athyriaceae sensu Tagawa & Iwatsuki (1972); <Athyriaceae sensu Ching (1978a); <Dryopteridaceae: Athyrioideae sensu Lovis (1978); <Dryopteridaceae: Phymatiae sensu Tryon & Tryon (1982); <Dryopteridaceae: Athyrioideae: Phymatiae sensu Kramer & al. (1990b); <Athyriaceae: Athyrioideae+Deparioideae+Diplazioideae sensu Wang & al. (2004); <Woodsiaceae sensu Smith & al. (2006); <Athyriaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial or epipetric, sometimes rheophytic; roots blackish, wiry, inserted radially, non-proliferous; rhizomes short- to long-creeping, or suberect to erect, branched or more commonly unbranched, bearing scales, and sometimes golden hairs similar to the root hairs (e.g., *Athyrium skinneri* (Baker) Diels); rhizome scales lanceolate, not or only weakly clathrate, the margins usually non-glandular, sometimes glandular (some *Deparia*), without distinct pubescence, entire or dentate, when present the teeth commonly formed by two adjacent cells (*Diplazium*); leaves sometimes internally mucilaginous (some *Deparia* and *Diplazium* spp., particularly those treated as *Callipteris*), not externally covered in mucilage during any stage of development, green in *Diplazium* and *Deparia*, the petiole and rachis frequently with a pink hue in *Athyrium* presumably due to anthocyanins, monomorphic, spirally arranged or sometimes distichous and dorsal (e.g., *Athyrium skinneri*), occasionally bulbiferous, closely to distantly spaced, sparsely to moderately scaly and occasionally pubescent (*Athyrium*, *Diplazium*) or with a reduction series beginning with scales at the base of the leaf that gradually reduce to catenate hairs distally (*Deparia*, some *Diplazium*); petioles castaneous, stramineous, or proximally darkened, often with a proximal thickening forming trochopods that may be starch-filled (*Athyrium*, *Cornopteris*, *Diplazium*), often with conspicuously elaborated aerophores (elsewhere termed pneumatophores; *Cornopteris*, some *Athyrium*, some *Deparia*), the bases usually persistent, rarely articulate to the rhizome (e.g., *Anisocampium* and *Athyrium skinneri*), and sometimes with golden hairs similar to the root hairs (e.g., *A. skinneri*); petiolar vascular bundles two (rarely more; Kato, 1972), each with hippocampiform xylem, the bundles distally uniting to form a single U- or V-shaped bundle; laminae soft-herbaceous to coriaceous, simple to 3-pinnate-pinnatifid, the apex usually pinnatifid or non-conform, sometimes conform in *Diplazium*, the leaf marginal cells differentiated into nodulose hyaline cells or not; pinna axes not articulate, sometimes muricate (*Diplazium*), sulcate adaxially, lacking a free central ridge; the rachis grooves V-shaped (*Anisocampium*, *Athyrium*, *Cornopteris*) or U-shaped (*Deparia*, *Diplazium*), continuous (*Anisocampium*, *Athyrium*, *Cornopteris*, most *Diplazium*) or not continuous (*Deparia*, some *Diplazium*), the sulcus wall of the rachis usually continuing as a prominent ridge onto the sulcus

wall of the costa (but not in *Deparia*); veins free or sometimes anastomosing (*Deparia* species treated as *Dictyodroma*, and some *Diplazium*), the areoles without free included veinlets, usually terminating before the leaf margin, the vein endings slightly raised and expanded, or forming hydathodes, or not differentiated; sori usually elongate, sometimes round, not terminal, on top of the vein, or along one side, singular or paired back-to-back along the same vein, or hooked in most *Athyrium* (i.e., paired back-to-back and crossing over the vein at one end in J- or U-shapes), or rarely sori marginal (e.g., *Deparia prolifera* (Kaulf.) Hook. & Grev.), at the tips of vein endings, usually indusiate; soral receptacle flat; indusia lateral, vaulted or essentially flat, glabrous or glandular, opening along the lateral margin; sporangia with stalks two or three cells wide in the middle; spores monolete, non-chlorophyllous, brown, the perispore nearly plain to coarsely tuberculate, echinate, or folded, the folds short and low, forming a rugate surface, or broad and wing-like; chromosome base numbers $x = 40$ (*Athyrium*, *Deparia*, some *Cornopteris*; Manton & Sledge, 1954; Kato, 1979; Sano & al., 2000a, b; Liu & al., 2011), or 41 (*Diplazium*, some *Cornopteris*; Manton & Sledge, 1954; Kato, 1979; Dawson & al., 2000). Reports of $x = 41$ for *Deparia* require confirmation (reviewed in Sano & al., 2000a), and reports for individual *Cornopteris* species are occasionally inconsistent (alternating between $x = 40$ and $x = 41$), indicating that further cytological study is needed.

Several genera of Athyriaceae can be diagnosed by unique or rare character states. However, character state reversals and homoplasy render these characters imperfect diagnostics for the family. *Deparia* typically has broad scales present at the base of the leaf that transition along a homologous series to septate hairs. Similar hairs occur in *Diplazium* (species treated in *Calopteris* by Pacheco & Moran, 1999), *Acystopteris*, and some species of *Woodsia* (e.g., *W. mollis*)—other species of *Woodsia* have septate hairs, but these are not reduced from broad scales. Many eupolypod II ferns have reduced filiform scales, but in most cases these never approach the septate hairs found in *Deparia* (see Fig. 3 in Sano & al., 2000b). *Deparia* also differs from most Eupolypods II in having sulcate rachises that are not continuous with the sulcae of the pinna costae. Many *Athyrium* and *Cornopteris* species have red-tinged leaves. This color is visible in live plants as well as on herbarium specimens. Blechnaceae also have reddish leaves and this has been attributed to the presence of anthocyanins (Crowden & Jarman, 1974). That family, and the other eupolypod II families with reddish leaves, differ in that the red coloration is present only in developing leaves and is not visible by maturity.

Another useful character of limited distribution is the corniculae/scales that are present adaxially at the junction of the pinna costa and the rachis in many *Athyrium* and *Cornopteris*. In addition, many *Athyrium* and some *Diplazium* species have small epidermal spinules along the adaxial pinna costae. Outside of the Athyriaceae, adaxial corniculae occur only in Rhachidosoraceae and *Onocleopsis* (Onocleaceae). In the Eupolypods I, similar structures also occur in *Didymochlaena*, and outside of the Eupolypods similar structures occur in *Pteris* (Pteridaceae). Athyriaceae also frequently have well-developed

trophopods, which consist of a thickened petiole base that is often starch-filled, persistent upon the rhizome, and in some cases highly sclerified. The trophopods of some *Athyrium* and *Deparia* are additionally adorned with toothed or wing-like protuberances, referred to as pneumatophores by Iwatsuki (1970) and Kato (1984).

Biology and phylogeny. — Athyriaceae are mostly medium-sized understory terrestrial ferns, comprising three major clades that correspond to the subfamilies Athyrioideae, Diplazioideae, and Deparioideae of Wang & al. (2004; with the exception of *Diplaziopsis* and *Homalosorus*, which Wang & al. (2004) include in Diplazioideae, and which we place in Diplaziopsidaceae). This alliance of “athyriid”, “diplaziid”, and “depariid” ferns (Rothfels & al., 2012) has a long history; at some point they have all been treated in a broad concept of *Athyrium* (e.g., Copeland, 1947). The sister-group relationship of the athyriids and diplaziids, and they together as sister to the depariids, was anticipated first by Hiraoka (1978), suggested by the single-locus data of Sano & al. (2000a), and strongly supported by multi-locus molecular data (Schuettpelz & Pryer, 2007; Rothfels & al., 2012). Character evolution in Athyriaceae is complex, and the generic-level relationships within the two large clades (athyriids, diplaziids) need further investigation (e.g., Liu & al., 2011).

■ BLECHNACEAE Newman, Hist. Brit. Ferns, ed. 2: 8 (1844)

Blechnoids; Deer Ferns, Chain Ferns, and allies. Approximately 200 species in *Blechnum* L. s.l. (~150 spp.; incl. many potential segregates), *Brainea* J. Sm. (1 sp.), *Diploblechnum* Hayata (2 spp.), *Doodia* R. Br. (~15 spp.), *Pteridoblechnum* Hennipman (2 spp.), *Sadleria* Kaulf. (6 spp.), *Salpichlaena* J. Sm. (3 spp.), *Steenisoblechnum* Hennipman (1 sp.), *Stenochlaena* J. Sm. (8 spp.), and *Woodwardia* Sm. (14 spp.; incl. *Anchistea* C. Presl., *Lorinseria* C. Presl.); (Holttum, 1971b; Moran, 1990; Cranfill & Kato, 2003).

<Polypodiaceae: Pteridoideae + Polypodiaceae: Blechnoideae sensu Christensen (1938); =Dennstaedtiaceae: Blechnoideae sensu Holttum (1947); =Blechnaceae sensu Nayar (1970); <Blechnaceae + Pteridaceae sensu Tagawa & Iwatsuki (1972); =Blechnaceae sensu Pichi Sermolli (1977); =Blechnaceae + Stenochlaenaceae sensu Ching (1978a); =Blechnaceae sensu Lovis (1978); =Blechnaceae sensu Tryon & Tryon (1982); =Blechnaceae sensu Kramer & al. (1990a); =Blechnaceae sensu Smith & al. (2006); =Blechnaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial or climbing (by means of rhizomes in *Stenochlaena* and *Blechnum* sect. *Lomaria* (Willd.) Diels, or by leaves in *Salpichlaena*), rarely epiphytic or rheophytic; roots blackish, wiry, inserted radially, non-proliferous; rhizomes short- to long-creeping, suberect, or erect, sometimes massive and arborescent (*Blechnum* sect. *Lomariocycas* (J. Sm.) C.V. Morton, and *Sadleria*), branched, or more commonly unbranched, sometimes stoloniferous (*Blechnum* sect. *Eublechnum* Hook. & Baker), bearing scales; rhizome scales lanceolate to linear-lanceolate, non-clathrate, light-brown to blackish, the margins glandular or not, entire or dentate,

without distinct pubescence; leaves reddish when young, green at maturity, sometimes covered in mucilage when young (some *Blechnum*), monomorphic or dimorphic, spirally arranged, occasionally bulbiferous, the bulbils frequently in a distal pinna axil, leaves usually closely spaced, sparsely to densely scaly, sometimes pubescent, sometimes with glandular nectaries (e.g., *Stenochlaena palustris* (Burm. f.) Bedd., *Blechnum orientale* L.); petioles greenish to dark brown or atropurpureous, the bases not expanded, not articulate to the rhizome, usually not persistent; petiolar vasculature with two large bundles on the adaxial side of the petiole and an arc of smaller bundles on the abaxial side of the petiole, rarely petioles with only two bundles (e.g., *Woodwardia areolata* (L.) T. Moore), the larger bundles with hippocampiform-shaped xylem, distally uniting to form a single U-shaped bundle; laminae soft-herbaceous to more often coriaceous, pinnatifid to 2-pinnate-pinnatifid, the base with or without a series of reduced pinnae, the apex conform or not, the leaf marginal cells differentiated and scarious or membranaceous, or non-differentiated; pinna axes articulate (*Stenochlaena*), or usually non-articulate, pinna bases sometimes with conspicuous aerophores in *Blechnum*, the aerophores appearing as a low protuberance or elongate and vermiform (e.g., *Blechnum violaceum* (Fée) C. Chr.); rachis axes sulcate adaxially, rarely not (e.g., some *Woodwardia*), the sulcae not continuous onto the next order, lacking a free central ridge; veins anastomosing, or more commonly with costular areoles and otherwise free, the areoles without free included veinlets, reaching the leaf margin or terminating before it, the vein endings forming hydathodes, or not differentiated; sori elongate, along one side of the costular commissural vein, indusiate, or sori acrostichoid and exindusiate (*Stenochlaena*); soral receptacle flat; indusia lateral, essentially flat, glabrous or sometimes glandular, opening along the lateral margin with the opening facing the costa; sporangia with stalks more than one cell wide in the middle; spores monolete, occasionally chlorophyllous (e.g., *Blechnum nudum* (Labill.) Leurss.; Sundue & al., 2011), usually non-chlorophyllous, usually pale brown or tan, the perispore with sharp ridges, broad folds, echinulate, tuberculate, foliose, or nearly plain; chromosome base numbers $x = 27$ (*Pteridoblechnum*; Tindale & Roy, 2002), 29 (*Blechnum*; Walker, 1973a), 31 (*Blechnum*; Walker, 1973a), 32 (*Doodia*; Tindale & Roy, 2002), 33 (*Blechnum*, *Sadleria*; Walker, 1973a; Smith & Mickel, 1977; F.S. Wagner, 1995), 34 (*Blechnum*, *Woodwardia*; Manton & Sledge, 1954; Tryon & Tryon, 1982), 35 (*Brainea*, *Woodwardia*; Britton, 1964; W.H. Wagner, 1955; Aziz Bidin, 1995), 36 (*Blechnum*; Walker, 1973a), 37 (*Stenochlaena*; Manickam & Irudayaraj, 1988), or 40 (*Salpichlaena*; Walker, 1973b).

Blechnaceae are unique among ferns in having elongate sori along a sub-costular commissural vein that is parallel to the pinna costa, with an indusiate sorus that opens to face the costa. Other ferns with elongate sori lack a commissural vein, and have indusia that face the costa at a low angle (not parallel) or are exindusiate. Blechnaceae also differ from nearly all other Eupolypods II by having petioles with a vascular anatomy that resembles those of Eupolypods I. That is, in addition to the two large bundles on the adaxial side of the petiole, there is an arc

of smaller bundles along the abaxial side of the petiole. However, *Woodwardia areolata* is aberrant among Blechnaceae in having only two.

Some genera of Onocleaceae, such as *Matteuccia* and *Pentarhizidium*, have a strong superficial resemblance to Blechnaceae. Those genera can be differentiated by fertile leaves with a modified leaf margin that opens to face the costa and the indusium itself, which is inconspicuous and faces away from the costa. *Plagiogyria* (Cyatheales; see Fig. 1) also appears similar; the shape of the lamina, dimorphic leaves, and young leaves covered in mucilage are all reminiscent of *Blechnum* sect. *Parablechnum* (C. Presl.) T. Moore. Other characters of *Plagiogyria*, however, support its position among the Cyatheales, namely the sporangial capsule with an oblique annulus, trilete spores, and a perispore with well-formed rodlets.

Biology and phylogeny. — Blechnaceae are cosmopolitan, with a wide range of growth habits, including tall arborescent species, near-annual roadside weeds, and tropical lianas. Like their sister group, Onocleaceae, Blechnaceae have a high frequency of fertile/sterile leaf dimorphism. Many of the smaller Blechnaceae genera nest within *Blechnum* s.l. (Nakahira, 2000; Cranfill, 2001; Schuettpelz & Pryer, 2007). While generic circumscription remains incomplete, the family is well defined and historically stable (with the exception of *Stenochlaena*, which was of uncertain affinity prior to the availability of molecular data, a challenging situation further complicated by Christensen having included three widely divergent taxa in his original description of the genus; Christensen, 1906; Holttum, 1971b). Our circumscription is identical to that of Smith & al. (2006), who provide further information on this family.

■ ONOCLEACEAE Pic. Serm., *Webbia* 24: 708 (1970)

Onocleoids; Sensitive Fern, Ostrich Fern, and allies. Five species in *Matteuccia* Tod. (1 sp.), *Onoclea* L. (1 sp. with two varieties), *Onocleopsis* F. Ballard (1 sp.), and *Pentarhizidium* Hayata (2 spp.); (Gastony & Ungerer, 1997; Rothfels & al., 2012).

=Polypodiaceae: Onocleoidae sensu Christensen (1938); =“unplaced”: Onocleoidae sensu Holttum (1947); =Dryopteridaceae: Onocleoidae sensu Nayar (1970); =Onocleaceae sensu Pichi Sermolli (1977); =Onocleaceae sensu Ching (1978a); =Dryopteridaceae: Onocleoidae sensu Lovis (1978); =Dryopteridaceae: Onocleae sensu Tryon & Tryon (1982); =Dryopteridaceae: Athyrioideae: Onocleae sensu Kramer & al. (1990b); =Dryopteridaceae: Onocleae sensu Gastony & Ungerer (1997); =Onocleaceae sensu Smith & al. (2006); =Onocleaceae sensu Christenhusz & al. (2011).

Characters. — Plants terrestrial, often in wet or seasonally wet habitats; roots blackish, wiry, inserted radially, non-proliferous; rhizomes short-creeping, unbranched, and erect (up to 1 m tall in *Onocleopsis*), or long-creeping, and branched (*Onoclea*), rhizomes sometimes stoloniferous (*Matteuccia*), bearing scales; rhizome scales lanceolate, non-clathrate, brown, the margins eglandular, entire or dentate, without distinct pubescence; leaves greenish and not covered in mucilage during

any stage of development, dimorphic, spirally arranged, leaves usually closely spaced (sometimes distantly spaced in *Onoclea*), sparsely to densely scaly, sometimes pubescent; petioles greenish to stramineous, the bases not articulate to the rhizome, expanded and often starch-filled (forming trophopods), persistent on the rhizome, sometimes for decades, forming a massive protective sheath in *Matteuccia* and *Pentarhizidium*; petioles with two vascular bundles, the bundles with hippocampiform-shaped xylem, distally uniting to form a single U-shaped bundle; laminae herbaceous, pinnatifid to 1-pinnate-pinnatifid, the base with or without a series of reduced pinnae, the apex pinnatifid or non-conform, the leaf marginal cells scarious or not differentiated (*Matteuccia*); pinna axes not articulate; the rachis axes sulcate adaxially, the sulcae not continuous onto the next order, lacking a free central ridge; veins mostly reaching the leaf margin, or terminating before it in *Pentarhizidium*, free or anastomosing (*Onoclea*, *Onocleopsis*), the areoles without free included veinlets, the vein endings expanded in *Pentarhizidium*, otherwise not differentiated; sori orbicular, terminal on the vein, indusiate (except *P. intermedium* (C. Chr.) Hayata); soral receptacle raised, conical; indusia lateral, triangular, ephemeral; sporangia with stalks more than one cell wide in the middle; spores monolete, chlorophyllous, the perispore brown, perispore with broad folds and echinulae; chromosome base numbers $x = 37$ (*Onoclea*; Haufler & Soltis, 1986), 39 (*Matteucia*; Kurita, 1960), or 40 (*Onocleopsis*, *Pentarhizidium*; Tsai & Shieh, 1985; Gastony & Ungerer, 1997).

Onocleaceae can be diagnosed by having dimorphic leaves, petioles with two vascular bundles, and thickened petiole bases, chlorophyllous spores, and sori with conical receptacles. Blechnaceae appear similar, but differ by having petioles with more than two vascular bundles (except *Woodwardia areolata*, which has two) and that are not expanded at the base, leaves that are reddish when young, and indusia that open to face the costa.

Biology and phylogeny. — Onocleaceae are a small family, yet one of the most familiar to residents of the north-temperate zone. The family is noteworthy for the strong fertile/sterile leaf dimorphism of its members, their typically large size, chlorophyllous spores, and unusual distributions: *Matteuccia* is circumboreal; *Onoclea* is disjunct between eastern North America and eastern Asia; *Onocleopsis* is endemic to southern Mexico and Guatemala; and *Pentarhizidium* is limited to eastern Asia. Our circumscription is identical to that of Smith & al. (2006), who provide further information on this family.

■ KEY TO EUPOLYPOD II FAMILIES

1. Sori elongate, usually on one side of the vein, rarely paired back-to-back on a single vein, never curving over to the other side of the vein and forming a U- or J-shape; petioles with two vascular bundles, these united distally to form an X-shape as seen in cross-section, vascular bundles with xylem in the shape of a “C” as seen in cross-section; rhizome scales clathrate, rarely with darkened indurate lumens; sporangial stalks one cell wide in the middle ...
..... **Aspleniaceae**

1. Sori elongate or round, on top of the vein, on one side, paired back-to-back, or on one side of the vein and curving over to other side and forming a U- or J-shape; petioles with more than two vascular bundles, or if two, then these distally united to form a U- or V-shape as seen in cross-section, largest vascular bundles with hippocampiform-shaped xylem; rhizome scales non-clathrate (except Rhachidosoraceae, some Cystopteridaceae); sporangial stalks more than one cell wide in the middle, usually three cells wide..... 2
2. Petiole with more than two vascular bundles (two in some *Woodwardia*); sori elongate, parallel to the costa, on a sub-costular commissural vein connecting lateral veins, indusiate, with the opening facing the costa, or sori acrostichoid (*Stenochlaena*); leaves reddish when young, not reddish at maturity **Blechnaceae**
2. Petiole with two vascular bundles (rarely more in Athyriaceae and Thelypteridaceae); sori on, along, or at the apex of a lateral vein, round or elongate, never acrostichoid, if elongate then usually at an angle to the costa, when parallel to the costa, the indusium opening to face the segment margin (away from the costa) or exindusiate; leaves green in all stages, or if reddish when young, then reddish at maturity as well (except some Thelypteridaceae and *Onoclea sensibilis* L., which are reddish only when young) 3
3. Fertile leaves strongly dimorphic with sori protected by contracted and inrolled segment margins; spores chlorophyllous..... **Onocleaceae**
3. Fertile leaves holomorphic or partially dimorphic (some Thelypteridaceae), the segments weakly contracted and not inrolled; spores not chlorophyllous 4
4. Leaves pubescent (rarely lacking hairs), the hairs acicular, forked, stellate, or hamate; rhizome scales often bearing similar hairs along the margin and surfaces; indusia, when present, reniform and attached laterally; pinna base usually with a prominent aerophore, the aerophore raised, orbicular, elongate, or vermiform; leaves sometimes mucilaginous when young **Thelypteridaceae**
4. Leaves glabrous or pubescent, the hairs not acicular, simple, never forked or hamate; rhizome scales ciliate or denticulate, but not bearing hairs similar to the leaves; indusia, when present, attached basally or laterally, if laterally then elongate or a minute scale, not reniform; pinna base without a prominent aerophore; leaves never mucilaginous..... 5
5. Indusium attached basally, encircling the sorus, globose, or composed of multiple scale-like or filamentous segments **Woodsiaceae**
5. Indusium attached laterally, or if attached basally then not encircling the indusium, and composed of a single scale-like segment, or exindusiate 6
6. Sori round, indusiate, and the receptacle slightly raised and hardened, or sori slightly elongate (not more than 2× longer than wide), exindusiate, the soral receptacle flat; veins reaching segment margin; indusium, when present, basal, a minute hood-like scale, arching over the sorus, frequently deciduous **Cystopteridaceae**
6. Sori usually elongate, several times longer than wide, sometimes round (some Athyriaceae), indusiate, the soral

- receptacle flat; veins usually ending before segment margin; indusium lateral, vaulted or essentially flat, opening along the lateral margin, usually persistent 7
7. Rhizome scales clathrate; vein endings undifferentiated, neither expanded, raised nor forming hydathodes **Rhachidosoraceae**
7. Rhizome scales non-clathrate; vein endings differentiated, either thickened, raised, or forming hydathodes 8
8. Veins forming a sub-marginal collecting vein; leaf margin with a broad membranaceous border; pinna bases subcordate, the basiscopic lobes overlapping the rachis **Hemidictyaceae**
8. Veins free or anastomosing, but not forming a sub-marginal collecting vein; leaf margin scarious or undifferentiated, but not with a broad membranaceous border; pinna bases truncate, cuneate, or excavate, but not subcordate, and not overlapping the rachis 9
9. Sori usually along one side of the vein, rarely paired back-to-back; roots pale, fleshy; sori vaulted, the indusium often splitting apically prior to opening laterally; veins raised and cartilaginous on the adaxial side of the lamina **Diplaziopsidaceae**
9. Sori usually along both sides of the vein, either paired back-to-back, or crossing over the vein and U- or J-shaped (on top of the vein in *Cornopteris* and some *Athyrium*); roots blackish, wiry; sori usually flat, sometimes vaulted, indusium never splitting apically prior to opening laterally; veins often expanded, but not raised or cartilaginous on the adaxial side of the lamina **Athyriaceae**

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