

What We Do (and Don't) Know About Ferns: *Dryopteris* (Dryopteridaceae) as a Case Study

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Abstract—Ferns are the second largest group of vascular land plants after the angiosperms, but remain chronically underrepresented in studies of plant phylogeny, biogeography, physiology, and genomics. The genus *Dryopteris*, the woodferns, is a large group with a worldwide distribution, and recent research has made it one of the better understood fern genera and a potential model for understanding many aspects of fern biology and evolution. Here we review historical and current understanding of the genus, and outline promising avenues of future research in ferns for which *Dryopteris* is an ideal study system, particularly for research on polyploid complexes, biogeographic distributions, and physiological ecology.

Keywords—Biogeography, hybridization, morphology, phylogeny, physiology, polyploidy, taxonomy.

Dryopteris Adans., commonly known as the wood, shield, or buckler ferns (Fig. 1), is a large leptosporangiate fern genus consisting of ca. 300–350 (Fraser-Jenkins 1986; Lu 1993; Zhang et al. 2012) or even 400 (Zhang et al. 2013) species. The genus is the third largest in the family Dryopteridaceae, itself the largest family of ferns (Smith et al. 2006; Zhang et al. 2013). *Dryopteris* species can be found worldwide in temperate and montane tropical regions, with a primary center of diversity in eastern Asia, and secondary centers in eastern North America, Mexico, South Africa, and western Europe. Historically, North American members of the genus have received much attention due to the hypothesized origins of several taxa via allopolyploid hybrid speciation, long thought to be a classic example of reticulate evolution. In recent years the efforts of a number of researchers have made *Dryopteris* one of the better-understood fern genera (e.g. Geiger and Ranker 2005; Li and Lu 2006a; Ekrt et al. 2010; Juslén et al. 2011; Sessa et al. 2012a, b, c; Zhang 2012; Zhang and Zhang 2012; Zhang et al. 2012; Roux 2012; Lee and Park 2013; Sessa and Givnish 2014; Testo et al. 2015), and have positioned it as a potential model for understanding biogeographic patterns and the dynamics of polyploid complexes in ferns. Ferns, with ca. 9,000 species (Schuettpelz and Pryer 2009), are the second largest group of vascular land plants after the angiosperms, but have historically received far less attention than the flowering plants. As sister to the seed plants, ferns occupy an important evolutionary position (Sessa et al. 2014), and they are characterized by unique aspects of their biology and natural history, including large genome sizes (Leitch et al. 2005; Bainard et al. 2011; Garcia et al. 2013) and high chromosome numbers (Manton 1950; Britton 1953, 1974; Nakazato et al. 2008), separate gametophytic and sporophytic stages of the life cycle, and relatively low levels of physiological performance (i.e. low maximum photosynthetic rates and hydraulic conductances) compared to angiosperms (Brodribb and Holbrook 2004; Brodribb et al. 2007; Watkins et al. 2010). Ferns have long been thought to be particularly prone to hybridization and polyploidy (Grant 1981), and Wood et al. (2009) recently calculated that 31% of speciation events in ferns are accompanied by a change in ploidy level. Despite

this, we still know relatively little about the effects of polyploidy on fern genome organization, despite rapid advances in our understanding of these processes in seed plants and angiosperms (e.g. Jiao et al. 2011).

In this review, we summarize past and present understanding of the genus *Dryopteris*, and use *Dryopteris* as an example to suggest a number of avenues for future research in ferns where basic understanding is still lacking. We begin with an overview of early studies on the genus, and then present our current understanding of phylogeny, evolutionary and biogeographic history, and hybridization and polyploidy for groups in major geographic regions of the world. Finally, we extend what we know about *Dryopteris* to explore what we still don't know about ferns generally, and suggest research directions that will be essential, both in *Dryopteris* and other genera, for understanding the unique biology and evolution of this lineage of plants.

THE GENUS *DRYOPTERIS*

Early Work on *Dryopteris* and Dryopteridaceae—The name *Dryopteris* was given by French naturalist Michel Adanson in his *Familles naturelles des plantes* (Adanson 1763), but extensive movement of taxa by researchers into and out of the genus over the years has led to a contemporary *Dryopteris* quite different from Adanson's. As with numerous other fern genera, many of the species now included in modern *Dryopteris* were historically placed in an enormous family Polypodiaceae (Pichi-Sermolli 1973; Fraser-Jenkins 1986). A number of these taxa were moved to the large family "Aspidiaceae" (nom. illeg.) by the late 1800s and early 1900s, and modern families and genera subsequently began to take shape. Carl Christensen, who worked extensively on tropical American *Dryopteris*, was the first to separate the thelypteroid and dryopteroid taxa of "Aspidiaceae" (Christensen 1906, 1913, 1920). Ching continued work on the thelypteroids and later proposed the family Thelypteridaceae (Ching 1936, 1940, 1963), while Holttum separated the dryopteroids into Dennstaedtiaceae subfamily Dryopteridoideae (Holttum 1947, 1949, 1959). Eventually, the former family "Aspidiaceae" was separated into the modern families Athyriaceae, Dryopteridaceae,

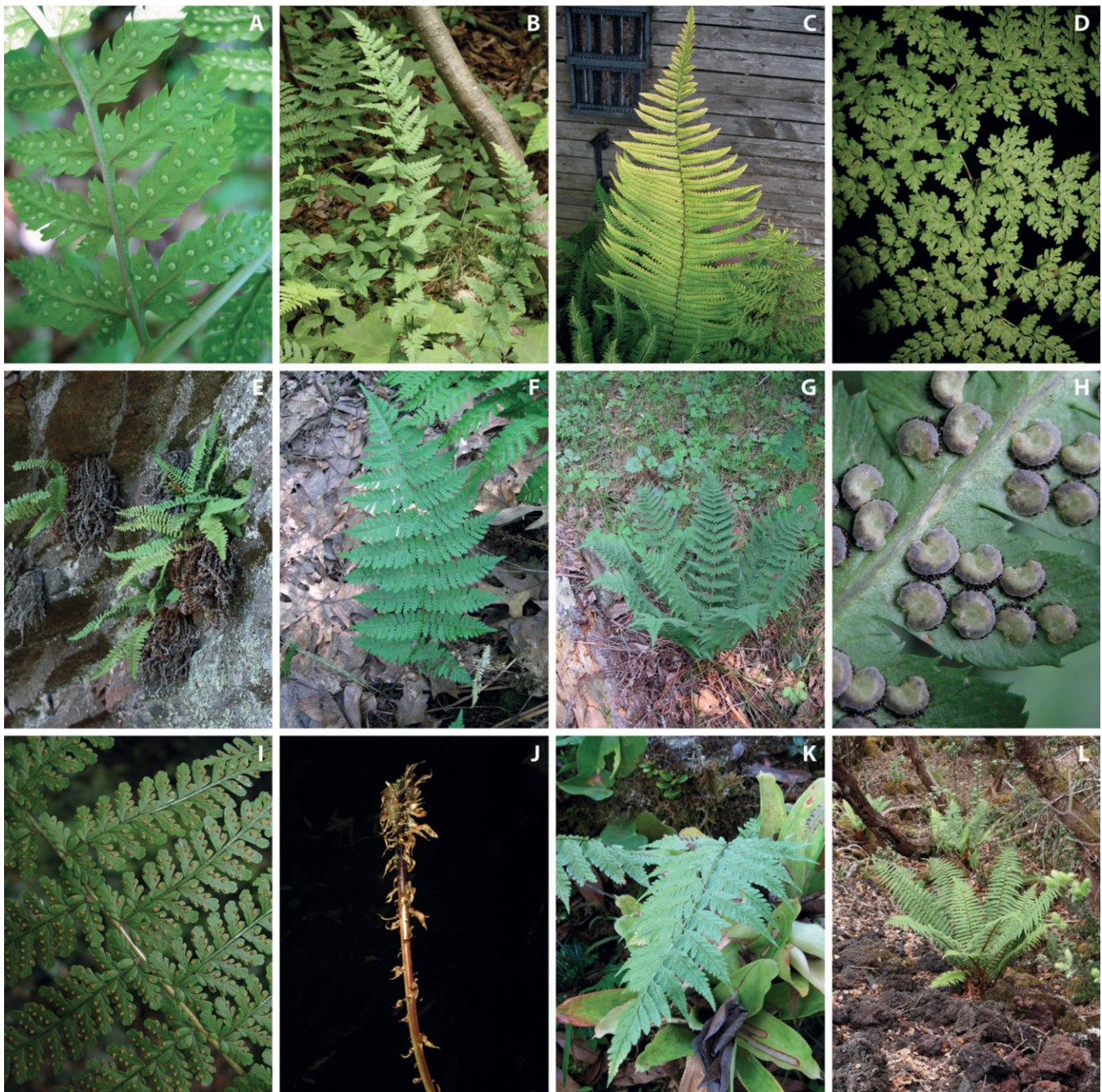


FIG. 1. Photographs of representative *Dryopteris* taxa. A. Immature sori of *D. carthusiana*. B. *D. cristata*. C. *D. cycadina*. D. *D. diffracta*. E. *D. fragrans*. F. *D. intermedia*. G. *D. marginalis*. H. Mature sori and sporangia of *D. marginalis*. I. *D. paleolata*. J. Stipe scales of *D. paleolata*. K. *D. patula*. L. *D. wallichiana*. A–C, E–H, K–L by E. B. Sessa; D, I–J by L.-B. Zhang.

Hypodematiaceae, Lomariopsidaceae, Onocleaceae, and Woodsiaceae, as well as Elaphoglossaceae and Peranemataceae (Ching 1940, 1965, 1975; Alston 1956; Pichi-Sermolli 1968, 1970a; Fraser-Jenkins 1986). Elaphoglossaceae and Peranemataceae were later combined with Dryopteridaceae and the latter given nomenclatural preference (Pichi-Sermolli 1970b). Subsequent phylogenetic analyses (Li and Lu 2006a, b; Liu et al. 2007) have identified four major lineages in Dryopteridaceae, which is now recognized as containing ca. 25 genera (Zhang et al. 2013). Recently, Christenhusz and Chase (2014) proposed a revision to fern classification in which Dryopteridaceae was combined with five other families comprising eupolypods I

sensu Smith et al. (2006) into a single family Polypodiaceae, reminiscent of the previous system that was abandoned roughly 100 yr ago (Pichi-Sermolli 1973). We agree with other recent authors (Sundue et al. 2014) that this decision runs contrary to major advances in fern classification of the last decade, and inhibits understanding of relationships among ferns rather than clarifying them. We advocate use of the established and widely accepted classification for ferns found in Smith et al. (2006, 2008).

Dryopteris itself has transformed considerably since the early 1900s, with numerous taxa transferred to other genera while a smaller number have moved in. Its largest reckoning

seems to have been Christensen's reference to "nearly 1,000" species of *Dryopteris* treated in his *Index filicum* (1906); around 300–400 species are now recognized in modern *Dryopteris* (Fraser-Jenkins 1986; Lu 1993; Zhang et al. 2012, 2013). Genera segregated from *Dryopteris* or which received taxa from it over the course of the 20th century include *Ctenitis* (C. Chr.) C. hr., *Lastrea* Bory, *Lithostegia* C. Presl, *Nephrodium* Michx., *Stenolepia* Alderw., *Stigmatopteris* C. Chr., and *Tectaria* Cav. (Fraser-Jenkins 1986). Within *Dryopteris*, subgeneric and sectional classification has been addressed by several authors, notably Itô (1935, 1936) who treated the Japanese and Taiwanese taxa, Ching (1938) who treated the Himalayan taxa including some Chinese, Indian, and Sri Lankan species, and Lu (1990a, b, 1999), Wu and Lu (2000), and Wu et al. (2013), who further revised the Chinese taxa. Fraser-Jenkins (1986) carried out the first and most intensive taxonomic study on *Dryopteris* worldwide. He divided the 225 species he recognized into four subgenera: *D.* subg. *Dryopteris*, *D.* subg. *Erythrovariae* (H. Itô) Fraser-Jenk., *D.* subg. *Nephrocystis* (H. Itô) Fraser-Jenk., and *D.* subg. *Pycnopteris* (T. Moore) Ching, and the first three of these further into 16 sections. His classification was a breakthrough and has been adopted and discussed widely (e.g. Lu 1990a, b, c, 1991a, b, 1993, 1999; Wu and Lu 2000; Geiger and Ranker 2005; Li and Lu 2006a; Sessa et al. 2012a; Zhang and Zhang 2012; Zhang et al. 2012; Wu et al. 2013).

Current Phylogeny and Taxonomy—Since Fraser-Jenkins' (1986) classification, confusion has lingered about the relationships between *Dryopteris* and several other genera. The relationships between *Dryopteris* and *Nothoperanema* (Tagawa) Ching, *Acrophorus* C. Presl, *Diacalpe* Blume, and *Peranema* D. Don have been particularly problematic; the latter three genera have together been considered a separate family (the Peranemataceae, sensu Ching 1978), and *Nothoperanema* a subgenus of *Dryopteris* (Tagawa 1938). In addition, several authors have recently found *Dryopteris* to be paraphyletic relative to *Acrorumohra* (H. Itô) H. Itô, *Dryopsis* Holttum & P. J. Edwards, and *Revwattsia* D. L. Jones (Li and Lu 2006b; Liu et al. 2007; Zhang et al. 2012; McKeown et al. 2012). Several groups have recently taken steps toward a revision of the genus based on these phylogenetic analyses: Zhang and Zhang (2012) resurrected *Dryopteris* subg. *Nothoperanema* (Tagawa) Li Bing Zhang, including within it all species that had been in the genera *Acrophorus*, *Diacalpe*, *Nothoperanema*, and *Peranema*; McKeown et al. (2012) transferred the monotypic *Revwattsia fragilis* (Watts) D. L. Jones to *Dryopteris* as *Dryopteris watsii* M. McKeown, Sundue & Barrington; Zhang (2012) placed *Dryopsis* as a new section within *Dryopteris* subg. *Erythrovariae* (*D.* sect. *Dryopsis* (Holttum & P. J. Edwards) Li Bing Zhang); and He et al. (2013) placed *Acrorumohra* as *D.* sect. *Acrorumohra* (H. Itô) Li Bing Zhang & H. He.

To date, no exhaustive phylogenetic analysis of all 350 + species of *Dryopteris* has been undertaken. However, studies of ca. 60 taxa by Geiger and Ranker (2005) and Li and Lu (2006a, b), and of ca. 100 taxa by Sessa et al. (2012a) and Zhang et al. (2012) strongly suggest that further revisions of the currently recognized supraspecific taxa (subgenera and sections of Fraser-Jenkins 1986) are in order. Sessa et al. (2012a) found 14 out of 20 supraspecific *Dryopteris* taxa to be non-monophyletic but did not have adequate sampling to test monophyly of several others, while Zhang et al. (2012), with better sampling across all supraspecific taxa, found 19 out of 20 to be non-monophyletic. Zhang et al. (2012)

also identified 13 well-supported clades within *Dryopteris* s. lat. that are supported by morphological synapomorphies and may serve as the basis for a future taxonomic revision of the genus. To date, less than half of the taxa potentially belonging to *Dryopteris* have been included in phylogenetic analyses, and so such a revision awaits more comprehensive sampling.

DRYOPTERIS IN THE AMERICAS

Taxonomy and Phylogeny—The American *Dryopteris* taxa have received much attention since the early 20th century from amateur and professional botanists alike. In his monograph on the tropical American *Dryopteris* taxa, Carl Christensen included 347 species and referred to another 17 in North America (Christensen 1913; 1920). The vast majority of these are now placed in other genera, and we currently recognize 16 species in Central and South America and 13 in North America (Montgomery and Wagner 1993; Mickel and Smith 2004; Sessa et al. 2012a). Two species are found in both regions, for a total of 27 New World *Dryopteris*.

The 13 sexual North American species include diploids, tetraploids, and one hexaploid, which belong to four sections within Fraser-Jenkins' *D.* subg. *Dryopteris* (Fraser-Jenkins 1986; Sessa et al. 2012a). The Central and South American taxa include species from *D.* subg. *Nephrocystis* sect. *Purpurascens* Fraser-Jenk. and *D.* subg. *Dryopteris* sects. *Cinnamomeae* Fraser-Jenk., *Fibrillosae* Ching, and *Pallidae* Fraser-Jenk. Additional Central and South American species unplaced by Fraser-Jenkins (1986) likely belong in his *D.* sect. *Cinnamomeae* (Mickel and Smith 2004; Sessa et al. 2012a), though these placements may change with future adjustments to the classification. Recent phylogenetic analyses (Sessa et al. 2012a, c) have shown that the North American *Dryopteris* taxa are not a monophyletic group, but that the majority of the Central and South American species do form a single strongly supported clade. The North American taxa are generally more closely related to European or Asian species, and at least one is sister to an African species (Sessa et al. 2012a). In plastid-based phylogenetic analyses, 11 of the 16 Central and South American species form a clade that is derived from an Asian ancestor via long-distance dispersal to the Americas (Sessa et al. 2012a). The phylogenetic relationships of all taxa in the Americas are dominated by reticulate evolution (Sessa et al. 2012b, c). For the Central and South American species, complex reticulate relationships involving Asian progenitors make clade-level associations particularly difficult to assess (Sessa et al. 2012c).

Distribution Patterns and Biogeography—The 27 New World species of *Dryopteris* fall into two groups: the 13 species in North America north of Mexico (Montgomery and Wagner 1993), and the 16 that occur in Mexico, throughout Central America, and into northern South America (Mickel and Smith 2004). Two taxa, *D. arguta* (Kaulf.) Maxon and *D. filix-mas* (L.) Schott, are shared between these two groups and are included in both counts, though both reach their southern range limit in northern Mexico. The North American species are most closely related to species from Europe, Africa, and Asia (Sessa et al. 2012a), and their current distributions appear to be largely the result of vicariance processes that broke up formerly continuous ranges that spanned these regions (though some species appear to be

the products of long-distance dispersal to North America; Sessa et al. 2012a). In contrast, the majority of the Central and South American species form a clade whose ancestor is inferred to have arrived in Central America via long-distance dispersal from Asia at least 32.3 million years ago (Sessa et al. 2012a). Subsequent movements to South America and back to Central America across the Isthmus of Panama are thought to have shaped these species' modern ranges.

Several of the North American taxa (specifically those with vicariant histories) continue to occupy broad ranges throughout North America as well as in Europe and Asia, including *D. carthusiana* (Vill.) H. P. Fuchs, *D. cristata* (L.) A. Gray, *D. expansa* (C. Presl) Fraser-Jenk. & Jermy, *D. filix-mas*, *D. fragrans* (L.) Schott, and *D. intermedia* (Willd.) A. Gray (Montgomery and Wagner 1993; Blockeel 2006). The remaining species are endemic to North America (Montgomery and Wagner 1993). The majority of the Central and South American species are endemic to that region (Mickel and Smith 2004), the only exception being *D. wallichiana* (Spreng.) Hyl. This taxon, which has a nearly circumtropical range, is thought to include multiple ploidy levels and possibly apomictic forms (Loyal 1959; Geiger and Ranker 2005), and is in great need of further study. Another apomictic taxon, *D. muenchii* A. R. Sm. (Reyes-Jaramillo et al. 2008), is endemic to cloud forests in Mexico (Mickel and Smith 2004), though it appears to have close relatives among the members of the "*D. semicristata*" complex in Europe and North America (see below) (Sessa et al. 2012a, c). In North America, the highest number of *Dryopteris* species is found in the temperate forests along the eastern coast, particularly in the New England and mid-Atlantic states of the U.S.A., and in New Brunswick, Quebec, and eastern Ontario provinces in Canada, with far fewer species in the southeast, mid-west, and western parts of the U.S.A. and in mid and western Canada. A second diversity hotspot in the Americas is in Mexico, where 13 species occur (Mickel and Smith 2004). The majority of these occupy ranges that extend throughout Central America, with species gradually falling out as they reach northern South America. The farthest south any *Dryopteris* can be found is in Peru and Bolivia (Tryon and Stolze 1991; Rojas Alvarado 2001), where they apparently reach the limits of their preferred temperate and montane tropical habitats. No species of *Dryopteris* are found, for example, in the lowlands of Amazonia.

Reticulate Evolution—Reticulate evolution has long been thought to have played a role in the evolution of North American *Dryopteris*, and many researchers have attempted to elucidate the history and relationships of the four extant diploids ($2n = 82$) and five putative allopolyploids (four tetraploids, $2n = 164$, and one hexaploid, $2n = 246$) in this complex (Crane 1953; Widén and Sorsa 1969; Widén and Britton 1969, 1985; Wagner 1971; Hickok and Klekowski 1975; Gibby and Walker 1977; Juslén et al. 2011). Chemotaxonomic studies played an important role in the early stages of this work, and in understanding the relationships of *Dryopteris* hybrids in North America generally (Widén and Britton 1971a; Britton and Widén 1974; Widén et al. 1975a). Together, this body of work resulted in several competing hypotheses to explain the provenance of the allopolyploids (Sessa et al. 2012b), one of which, the so-called "semicristata" hypothesis, has recently been validated using plastid and nuclear DNA sequencing data (Sessa et al. 2012b). This explanation for these species' relationships involves a "missing," putatively extinct diploid progenitor of two of

the allotetraploids, "*Dryopteris semicristata*" (Walker 1955; 1961). Of the remaining four North American species not involved in the reticulate complex, another one, *D. filix-mas*, is also thought to have reticulate origins, and possibly to harbor multiple ploidy levels (Widén and Britton 1971b; Fraser-Jenkins and Corley 1972; Fraser-Jenkins and Widén 2006; Sessa et al. 2012b). There have also been at least 25 sterile hybrid combinations reported in North American *Dryopteris*, many of them triploids with $2n = 123$; this is more hybrids than are known for any other fern genus on the continent (Montgomery and Wagner 1993).

The Central and South American *Dryopteris* species appear to have experienced a reticulate history even more complex than that in North America. The majority of these taxa have multiple copies of the nuclear marker *pgiC* (Sessa et al. 2012c), one or more of which are most closely related to *pgiC* sequences found in contemporary Asian species, though the taxa possessing them are endemic to the Americas. Sessa and colleagues (Sessa et al. 2012c) hypothesized that this pattern has resulted from hybridization in Asia followed by long-distance dispersal to the Americas, where additional hybridization events and backcrossing resulting in chloroplast capture have occurred (Sessa et al. 2012c). This complex scenario needs additional testing and confirmation via further nuclear genomic sequencing, and flow cytometry or chromosome squashes to confirm whether the Central and South American taxa are in fact polyploids.

DRYOPTERIS IN EUROPE

Taxonomy and Phylogeny—The European *Dryopteris* flora has been relatively well known for decades (Jalas and Suominen 1972). Blockeel (2006) recognized 22 species and subspecies of *Dryopteris*, and the most recent Euro+Med PlantBase list includes 30 species and ten subspecies, for a total of 38 taxa (Christenhusz and von Raab-Straube 2013). This database includes Euro-Caucasian, Mediterranean, and Macaronesia taxa. *Dryopteris ardechensis* Fraser Jenk. is discussed but not included in the key, and the Cape Verdean endemic *D. gorgonea* J. P. Roux is currently listed as part of the European flora (Blockeel 2006). In the 1970s to early 1980s, five new taxa or combinations were added to the flora: *D. tyrrhena* Fraser-Jenk. & Reichst. (Fraser-Jenkins et al. 1975), *D. guanchica* Gibby & Jermy and *D. crispifolia* Rasbach, Reichst. & G. Vida (Gibby et al. 1977), *D. submontana* (Fraser-Jenk. & Jermy) Fraser-Jenk. (Fraser-Jenkins 1977), and *D. corleyi* Fraser-Jenk. (Fraser-Jenkins 1982). *Dryopteris lacunosa* S. Jess., Zenner, Chr. Stark & Bujnoch was the most recent addition to the European *Dryopteris* flora (Jessen et al. 2011).

A number of subspecies have been recognized for the European taxa. Christenhusz and von Raab-Straube (2013) recognized subspecies for *D. affinis* (Lowe) Fraser-Jenk. (5), *D. intermedia* (2), and *D. cambrensis* (Fraser-Jenk.) Beitel & W. R. Buck (4). Blockeel (2006) recognized seven subspecies of *D. intermedia* in Europe including *D. intermedia* subsp. *maderensis* (Alston) Fraser-Jenk. and subsp. *azorica* (H. Christ) Jermy, whose taxonomic levels have varied between different authors. Gibby (1979) included both as species, while Fraser-Jenkins (1982) treated subsp. *maderensis* as a subspecies and subsp. *azorica* as a species, and in 1986 (Fraser-Jenkins 1986) treated both as subspecies. Christenhusz and von Raab-Straube (2013) accepted these as the only

two subspecies of *D. intermedia* in Europe. *Dryopteris mindshelkensis* N. Pavl. and *D. schorapanensis* Askerov have been treated in most floras as subspecies of *D. villarii* (Bellardi) Schinz & Thell. and *D. affinis*, respectively, but were considered species by Christenhusz and von Raab-Straube (2013).

The European *Dryopteris* flora consists of species belonging to one subgenus, *Dryopteris*, as classified by Fraser-Jenkins (1986). However, as the classification has been challenged by recent molecular phylogenetic analyses (Sessa et al. 2012a, c; Zhang and Zhang 2012; Zhang et al. 2012), the European group will likely come to include members of multiple subgenera and sections. Recent large phylogenetic analyses based on plastid (Geiger and Ranker 2005; Li and Lu 2006b; Sessa et al. 2012a, c; Zhang et al. 2012) and nuclear markers (Juslén et al. 2011; Sessa et al. 2012c), have shown that European *Dryopteris* are not a monophyletic group. In the most recent and extensive studies including European accessions, the European species fall into four of five large, monophyletic clades (Sessa et al. 2012a, c). One of these clades consists solely of the circumboreal species *D. fragrans*, which is sister to all other *Dryopteris* species. In the 100 species sampling of Zhang et al. (2012) which identified 13 major evolutionary lineages, nine European species were represented, which were placed in five different clades.

Distribution Patterns and Biogeography—*Dryopteris* is the second largest genus of ferns in Europe. Of the Euro-Mediterranean taxa, six are widely distributed in the northern hemisphere, including *D. carthusiana*, *D. cristata*, *D. expansa*, *D. filix-mas*, *D. fragrans*, and *D. intermedia*. There are about 20 taxa endemic to mainland Europe, a few of which have limited distributions in northern Africa. Five taxa occur around the Black Sea including in the Caucasus, and five are endemic to the Macaronesian Islands. In his monograph of *Dryopteris* in Spain, Portugal and Macaronesia, Fraser-Jenkins (1982) lists 19 species, and Salvo and Arrabal (1986) included 13 for the Iberian flora; the Euro+Med distribution maps include 15 species distributed in this region (Christenhusz and von Raab-Straube 2013). Davis (1965) listed seven taxa in the Turkish flora, which now includes 13 species (Christenhusz and von Raab-Straube 2013). Fraser-Jenkins and Reichstein (1984) included nine taxa in the Central European flora that now includes 17 species (Christenhusz and von Raab-Straube 2013), and Stace (1991) listed 10 species in his flora of the British Isles, which now includes 17 species and subspecies (Christenhusz and von Raab-Straube 2013). The European boreal *Dryopteris* flora consists of seven species (Fedorov 1999; Sarvela and Fraser-Jenkins 2000; Christenhusz and von Raab-Straube 2013). These numbers reflect that most of the diversity of European *Dryopteris* is in the southern, Mediterranean region, and the number of species diminishes gradually from south to north. In-depth historical biogeographic studies of the entire European *Dryopteris* flora have not yet been undertaken, but Jermy (1984) postulated that of 16 species in the Mediterranean area, 12 evolved in Southern Europe or spread from West-Central Asia or Macaronesia. Kalliola (1937) concluded that *D. fragrans* had a much larger distribution in Kola and Finnish Lapland during the early postglacial period, when the climate was more continental than at present. The last ice age and colder climate period around 10,000 BP has affected the biogeographic history of the European flora severely (Hewitt 1999); Scandinavia and much of the British Isles were covered by ice and Central

Europe had tundra conditions during most of that time. Many plant groups remained in southern refugia during the ice age and gradually spread northward following glacial retreat so that their present distributions were reached only around 6,000 BP (Hewitt 1999).

Dryopteris filix-mas is the species with the largest distribution, which extends throughout Europe in addition to having a broad range in Asia and North America (Blockeel 2006). The ranges of many other species also extend outside of Europe. In addition to *D. filix-mas*, another five European species are also found in North America (Juslén et al. 2011). The related biogeographic history of these species in Europe and North America is demonstrated by *D. intermedia*. The North American *D. intermedia* subsp. *intermedia* has been separated long enough to become distinct morphologically from the Madeiran endemic *D. intermedia* subsp. *maderensis*, and the Azorean endemic *D. intermedia* subsp. *azorica* (Jermy 1984). However, their chromosomes pair almost totally with one another (Walker 1961). Recent research on divergence times and historical biogeography of New World *Dryopteris* has given insights to the history of the European taxa as well (Sessa et al. 2012a). Divergence time estimates show that the ancestors of the circumboreal species *D. fragrans* and the rest of the genus diverged ca. 42 Ma (Sessa et al. 2012a). Vicariance has been responsible for the fragmented ranges of *D. cristata*, *D. expansa*, and *D. filix-mas* in Europe and North America, while long-distance dispersal explains the arrival in North America of *D. carthusiana* and *D. intermedia*.

Reticulate Evolution—As in North America, there are several examples of polyploidy and hybridization in the European *Dryopteris* flora (Sigel 2008; Juslén et al. 2011), some of which involve the same taxa as in North America. Around half of the *Dryopteris* species in Europe are diploid ($2n = 82$) and the other half are polyploids with chromosome numbers of either $2n = 123$ (triploids), $2n = 164$ (tetraploids), or $2n = 246$ (hexaploids) (Moore 1983). The basis for cytotoxic study of all European ferns, including *Dryopteris*, is Manton's (1950) study that revealed the ploidy levels of numerous widespread species. Following Manton's work, the first hypotheses of complex relationships of diploid and polyploid *Dryopteris* were presented in the cytological studies of Walker (1955, 1961) and Gibby and Walker (1977) for the "*D. semicristata*" complex. Studies by Gibby and co-workers (Gibby et al. 1977, 1978; Gibby and Walker 1977; Gibby 1979, 1983, 1985a) further explored the relationships of several *Dryopteris* occurring in Macaronesia and the Iberian Peninsula, including members of the *D. dilatata* (Hoffm.) A. Gray complex, resulting in one of the first hypotheses for reticulate evolution amongst those species. Extensive chemotaxonomic studies testing this hypothesis were carried out by Widén and co-workers (see e.g. Widén et al. 1970, 1971, 1975b, 1996; Euv et al. 1980; Widén and Britton 1985).

Recently, the relationships of various European species complexes have been further clarified by research employing molecular analyses. Jiménez and colleagues have explored genetic diversity between polyploids and diploids in the *D. aemula* (Aiton) Kuntze group (Jiménez et al. 2008, 2009, 2010), and Ekrt and colleagues (2010) used genome size to study species delimitation in the *D. carthusiana* complex. Phylogenetic analyses using nuclear locus *pgiC* have clarified the reticulate evolutionary history of European allotetraploids *D. carthusiana*, *D. cristata*, and *D. guanchica* (Juslén et al. 2011; Sessa et al. 2012b, c). The relationships of

D. crispifolia, *D. dilatata*, and *D. filix-mas* remain uncertain or have low support, though they too show evidence of reticulate evolution (Juslén et al. 2011; Sessa et al. 2012b, c). Apogamy is relatively common in *Dryopteris* (Hoshizaki and Wilson 1999) and there are several apomicts in the European flora, including *Dryopteris remota* (Döll) Druce (Schneller and Holderegger 1994; Schneller et al. 1998), *D. borrieri* (Newman) Oberh. & Tavel (Mehra and Loyal 1965), and members of the *D. affinis* complex (Fraser-Jenkins 1980; Menendez et al. 2006; Quintanilla and Escudero 2006; Schneller and Krattinger 2010).

DRYOPTERIS IN AFRICA

Taxonomy and Phylogeny—The African *Dryopteris* flora is relatively well-known, as the northern African species composition (Dobignard and Chatelain 2010) is very similar to that in the Mediterranean area (Fraser-Jenkins 1982), and the sub-Saharan species were recently revised by Roux (2012). Before Roux, Pichi-Sermolli was active in Africa (Pichi-Sermolli 1951, 1977, 1984, 1985), and named several species there. Fieldwork on ferns in Africa has not been intensive, and most of the collections studied by Roux were from the 1960s or earlier. He anticipated a need for taxonomic redefinitions once sufficient material became available for study from larger geographical areas (Roux 2012), and this remains a pressing need for many fern groups in addition to *Dryopteris*.

Northern Africa, from Morocco in the west to Egypt in the east, has eight species, two subspecies, and two hybrids of *Dryopteris* (Dobignard and Chatelain 2010). Of these, only *D. oligodonta* (Desv.) Pic. Serm. is also found in sub-Saharan Africa; the rest also exist in Europe. Sub-Saharan Africa has 26 *Dryopteris* species. Eleven of these, almost half of the flora, were newly described by Roux during the last decade or so (Roux 2002, 2003, 2004a, b, c, d, 2005). He listed eleven *Dryopteris* species present in the Indian Ocean islands, including Madagascar, La Réunion, Mauritius, and the Seychelles (Roux 2011), seven of which are endemic to this region (the rest are shared with mainland Africa). Roux also studied *Dryopteris* on the isolated Atlantic Ocean islands of St. Helena and Ascension (Roux 2013), which have two and one endemic *Dryopteris* species, respectively.

The sub-Saharan African species have been very poorly represented in phylogenetic analyses to date, largely due to the lack of recent collections. Six sub-Saharan *Dryopteris* species were resolved to three different clades by Sessa et al. (2012a), indicating a polyphyletic history. No morphological synapomorphies in support of these clades have so far been identified (Roux 2012). In addition, the northern African species have been represented entirely by collections from the Mediterranean area (e.g. Juslén et al. 2011), and the Atlantic Island taxa have never been included in a phylogenetic analysis.

Distribution Patterns and Biogeography—African *Dryopteris* species generally occupy one of three distinct distribution patterns, centered around northern Africa, western Africa, or southern and eastern Africa (Crouch et al. 2011; Roux 2012). Those taxa in northern Africa are generally found throughout the Mediterranean region and are likely most closely related to Mediterranean rather than to other African species. There is a high degree of endemism among the *Dryopteris* taxa in sub-Saharan Africa, Madagascar, and the

Atlantic islands, and many of these species have extremely restricted ranges (Roux 2011, 2012, 2013), though others have wide ranges within the distribution centers (Roux 2012). Almost all taxa in these regions occur in mountainous habitats, consistent with the inclination of the genus towards temperate and montane tropical localities; *Dryopteris* rarely occur in lowland tropics. *Dryopteris oligodonta* is the only species occurring in both northern Africa (Dobignard and Chatelain 2010) and sub-Saharan Africa (Cape Verde) (Roux 2012).

Reticulate Evolution—Relatively little is known about the frequency of polyploidization and hybridization among the African *Dryopteris* taxa. Of the northern African group, five species and one subspecies are diploids and three are tetraploids. Ploidy level is known for nine of the 26 sub-Saharan taxa, of which five are diploids, one is triploid, and three are tetraploids (Roux 2012). Roux (2012) found that guard cell length appears to reflect ploidy level in sub-Saharan *Dryopteris*, and based on his estimates of guard cell length (Roux 2012) there may be at least another nine African species that are polyploids. Whether these are allo- or auto-polyploids (i.e. the products of hybridization plus polyploidy or just polyploidy) is unknown, as the phylogenetics of African *Dryopteris* are to date totally unexplored.

DRYOPTERIS IN ASIA

Taxonomy and Phylogeny—Although *Dryopteris* appears to have diversified in every major geographic area of the world (except Antarctica) (Fraser-Jenkins 1986), its highest diversity is clearly found in the Sino-Japanese and Sino-Himalayan regions and neighboring areas in Asia (Fraser-Jenkins 1986; Iwatsuki 1995; Wu et al. 2013). There are about 250 species known from Asia and the Pacific islands. Understanding of the *Dryopteris* diversity in this region has been much improved through tremendous efforts over the past decades by many authors (Itô 1935, 1936; Ching 1938; Fraser-Jenkins 1986, 1989, 1994; Lu 1990a, b, c, 1991 a, b, 1993, 1999; Iwatsuki 1995; Wu and Lu 2000; Geiger and Ranker 2005; Zhang 2012; Zhang and Zhang 2012; Wu et al. 2013). As the geographic region with the largest number of *Dryopteris* taxa, the Asian and Pacific Island species are almost necessarily not monophyletic as a whole, though there are large groups of Asian species that do form clades (Sessa et al. 2012a).

All four subgenera and 15 out of 16 sections (except *Dryopteris* sect. *Cinnamomeae*) recognized by Fraser-Jenkins (1986) and one additional subgenus and five additional sections recognized by Zhang (2012) and Zhang and Zhang (2012) are represented by at least one species in Asia and the Pacific islands. All six species of *D.* subg. *Pycnopteris*, all 22 species of *D.* sect. *Dryopsis*, and all 50 species of *D.* subg. *Erythrovariae* are endemic to Asia (mainly China and Japan). Except for *D. squamiseta* (Hook.) Kuntze, all other 26 species of *D.* subg. *Nothoperanema* are endemic to Asia and the Pacific islands (Zhang and Zhang 2012). Seventeen species of *D.* subg. *Nephrocystis* occur in Asia and the Pacific islands, and about 130 species of *D.* subg. *Dryopteris* in ten sections sensu Fraser-Jenkins (1986) are distributed in this region.

The first morphological hypothesis on the infrageneric relationships of Asian and Pacific island *Dryopteris* was proposed by Itô (1935, 1936) when he studied Japanese species of *Dryopteris* and proposed *D.* sect. *Nephrocystis* H. Itô and *D.* sect. *Erythrovariae* H. Itô. Both of Itô's sections were adopted by Fraser-Jenkins (1986) and elevated to subgeneric

rank, though with different circumscriptions. The first comprehensive taxonomic work on Asian *Dryopteris* was conducted by Ching (1938), who classified 93 species of the genus in China and the Himalaya and neighboring areas into two subgenera, *D. subg. Pycnopteris* and *D. subg. "Eudryopteris C. Chr."*, and the latter into *D. sect. Fibrillosae* and *D. sect. "Bulligeriae Ching"* (= *D. sect. Erythrovariae* (H. Itô) Fraser-Jenk.).

In his series of studies of species of Yunnan, China, Lu (1990a, 1990b, 1990c, 1991a, 1991b, 1999) largely adopted Fraser-Jenkins' (1986) classification but recognized neither *D. subg. Nephrocystis* nor *D. sect. Polita* Fraser-Jenk., and re-classified a few Chinese species into different sections. In addition, Lu (1990a, b, 1999) also proposed three new sections: *D. sect. Caespitosae* S. G. Lu (Lu 1990a), *D. sect. Chrysocomae* S. G. Lu (1990b), and *D. sect. Indusiatae* S. G. Lu (1999). Wu and Lu (Wu and Lu 2000) classified 127 Chinese species of *Dryopteris* into three subgenera: *D. subg. Dryopteris*, *D. subg. Erythrovariae*, and *D. subg. Pycnopteris*, and the first and second subgenera further into three and 13 and three sections, respectively. Wu and Lu's (2000) classification is a modified version of Fraser-Jenkins' (1986) but the two classifications differ in the treatment of many Chinese species. Later, Wu et al. (2013) adopted *D. subg. Nothoperanema*, reinstated by Zhang and Zhang (2012), and divided 167 Chinese species into four subgenera and 22 sections, including four sections proposed by Zhang

and Zhang (2012): *D. sect. Acrophorus*, *D. sect. Diacalpe*, *D. sect. Nothoperanema*, and *D. sect. Peranema*.

Thirty-seven nomenclatural novelties (6 sections, 31 species) have been published in the past three years in the *Dryopteris* flora of Asia and the Pacific islands (Table 1), and additional taxonomic problems remain. Much material from China, Vietnam, and the Pacific islands needs further examination, and dozens of names from the region need to be treated taxonomically (Wu et al. 2013). Recently, Zhang and Zhang (2012) proposed the reinstatement of *D. subg. Nothoperanema*, composed of *Acrophorus*, *Diacalpe*, *Nothoperanema*, and *Peranema*. Taxonomic work on this subgenus has been conducted and 27 species recognized, 26 of which are endemic to Asia and the Pacific islands. Within *Dryopteris* subg. *Nothoperanema*, *D. sect. Peranema* is resolved as sister to the remaining three sections of the subgenus, followed by *D. sect. Nothoperanema* which in turn is resolved as sister to a clade containing *D. sect. Acrophorus* and *D. sect. Diacalpe*. However, support values for these relationships are not high (Zhang and Zhang 2012).

Distribution Patterns and Biogeography—The highest species diversity of *Dryopteris* globally is found in the subtropical regions of China, and generally the further one travels from this area, the poorer the *Dryopteris* diversity becomes. There are currently 175 species recognized for China (Wu et al. 2013), 69 in the Indian subcontinent (Fraser-Jenkins 1989), 49 in Taiwan (Knapp 2011), 66 in Japan (Iwatsuki 1995),

TABLE 1. Thirty-seven nomenclatural novelties (six sections, 31 species) published in 2012–2013 to the *Dryopteris* flora of Asia and the Pacific islands.

Nomenclatural addition	Reference
<i>D. sect. Acrophorus</i> (C. Presl) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. sect. Acrorumohra</i> (H. Itô) Li Bing Zhang & H. He	Wu et al. (2013)
<i>D. sect. Diacalpe</i> (Blume) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. sect. Dryopsis</i> (Holtum & P. J. Edwards) Li Bing Zhang	Zhang (2012)
<i>D. sect. Nothoperanema</i> (Tagawa) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. sect. Peranema</i> (D. Don) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. acrophorus</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. adscendens</i> (Ching ex S.H. Wu) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. annamensis</i> (Tagawa) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. crassirachis</i> (Ching) Li Bing Zhang	Zhang (2012)
<i>D. damingshanensis</i> Li Bing Zhang & H. M. Liu	Zhang and Liu (2013)
<i>D. diacalpe</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. diacalpioides</i> (Ching) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. dulongensis</i> (S. K. Wu & X. Cheng) Li Bing Zhang	Zhang (2012)
<i>D. emeiensis</i> (Ching) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. exstipellata</i> (Ching & S. H. Wu) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. grandifrons</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. hookeriana</i> (T. Moore) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. × holttumii</i> Li Bing Zhang	Zhang et al. (2013)
<i>D. jiucaipingense</i> P. S. Wang, Q. Luo & Li Bing Zhang	Luo and Zhang (2012)
<i>D. kungiana</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. leiboensis</i> Li Bing Zhang	Zhang (2012)
<i>D. liboensis</i> P. S. Wang, X. Y. Wang & Li Bing Zhang	Zhang et al. (2012)
<i>D. medogensis</i> (Ching & S. K. Wu) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. nidus</i> (Baker) Li Bing Zhang	Zhang (2012)
<i>D. nodosa</i> (C. Presl) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. nushanensis</i> Li Bing Zhang	Zhang (2012)
<i>D. paleolata</i> (Pic. Serm.) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. papuae-novae-guineae</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. peranema</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. pseudocaenopteris</i> (Kunze) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. raiateensis</i> (J. W. Moore) Li Bing Zhang	Zhang and Zhang (2012)
<i>D. submariformis</i> (Ching & Chu H. Wang) Li Bing Zhang	Zhang (2012)
<i>D. wantsingshanica</i> (Ching & K. H. Shing) Li Bing Zhang	Zhang (2012)
<i>D. wusugongii</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. wuzhaohongii</i> Li Bing Zhang	Zhang and Zhang (2012)
<i>D. zhuweimingii</i> Li Bing Zhang	Zhang and Zhang (2012)

ca. 20 in Vietnam, 14 in Thailand (Tagawa and Iwatsuki 1988; Zhang 2012), 16 in Sri Lanka (Sledge 1973), seven in Indonesia, six in Malaysia, nine in New Guinea and Papua New Guinea (Fraser-Jenkins 1986; Zhang 2012; Zhang and Zhang 2012), three in Australia (including *Revvattisia fragilis* (= *Dryopteris wattsi*)), and 11 in Hawaii (Palmer 2003). Many of the Asian and Pacific Island taxa have limited ranges or are endemic to those regions, but five are also found in Europe and North America: *Dryopteris carthusiana*, *D. expansa*, *D. filix-mas*, *D. fragrans*, and *D. wallichiana*. *Dryopteris squamiseta* (Hook.) Kuntze has the largest range, occurring in central and southern Africa, Madagascar, Bhutan, China (Xizang, Yunnan), Taiwan, India, and La Réunion (Zhang and Zhang 2012; Wu et al. 2013).

Reticulate Evolution—Knowledge of reticulate evolution of *Dryopteris* species in Asia and the Pacific islands is still very scarce and chromosome counts are lacking for the majority of taxa, but there has been one recent study on the *D. varia* complex using both nuclear and chloroplast genes (Hori et al. 2014). There have been a few studies on chromosome counts of Chinese *Dryopteris* (e.g. Wang and Zhang 1981; Wang and Xia 1984; Wang 1985; Xiang et al. 2006), and a few on those of Himalayan *Dryopteris* (e.g. Gibby 1985b). Japan is the best-studied region of *Dryopteris* for chromosomes in Asia and the Pacific islands. Hirabayashi (1974) did extensive early work on the cytology and cytogeography of Japanese species of *Dryopteris*, and of the 62 Japanese taxa (*Dryopteris* s.s. + *Acrophorus*) documented by Iwatsuki (1995), 25 species are diploid ($2n = 82$), 16 are triploid ($2n = 123$), four are tetraploid ($2n = 164$), eight contain a mixture of ploidy levels, and the rest are unknown. A particularly well-documented Asian polyploid complex is the *D. varia* (L.) Kuntze group, which includes at least nine species distributed in China, Korea, and Japan (Lee et al. 2006; Lee and Park 2013). Several species and species groups in Asia have apogamous members, including *D. chinensis* Koidz. (Kanamori 1967), *D. fuscipes* C. Chr. and *D. hondoensis* Koidz. (Kanamori 1972), and the *D. sparsa* (D. Don) Kuntze (Darnaedi and Iwatsuki 1987; Darnaedi et al. 1990) and *D. varia* complexes (Lin et al. 1992, 1995; Hori et al. 2014) in Japan. Most of the 36 species in *D.* subg. *Erythrovariae* sensu Fraser-Jenk. are thought to be apomictic (Fraser-Jenkins 1986; Widén et al. 2001). Natural hybridization is relatively common in *Dryopteris* in Asia and the Pacific islands. Twenty-four natural hybrids have been described from Japan (Iwatsuki 1995). In contrast, only a few hybrids have been described from China and Korea (e.g. Wang 1985; Fraser-Jenkins 1986). Fraser-Jenkins (1986) listed nine natural hybrids from the Indian Subcontinent and described one more later (Fraser-Jenkins 2008).

FUTURE DIRECTIONS: WHAT WE STILL DON'T KNOW ABOUT FERN BIOLOGY

The foregoing review of historical and current knowledge of *Dryopteris* suggests, we hope, a plant group that decades of research have told us much about, but for which large knowledge gaps persist nonetheless. Two such deficiencies concern the role of hybridization and polyploidy in generating taxonomic confusion, and the historical biogeography of taxa on a global scale. These are critical areas that apply broadly across ferns as well as in other plant groups, and which continue to pose challenges for researchers as the

available data, particularly molecular sequence data, have tended to generate more questions than they have answered.

In recent years researchers have sequenced ca. 220 *Dryopteris* species for between one and five plastid loci (Geiger and Ranker 2005; Juslén et al. 2011; Sessa et al. 2012a, c; Zhang et al. 2012). Despite these efforts, the backbone of the *Dryopteris* phylogeny and many small clades remain very poorly supported (Sessa et al. 2012a; Zhang et al. 2012). The single large-scale nuclear phylogeny produced for *Dryopteris* to date, based on one marker, also suffers from low support values (Sessa et al. 2012c). Given the age of the genus – ca. 42 million years (Sessa et al. 2012a) – and short lengths of many poorly supported branches, homoplasy and saturation issues may contribute to these low support values and lack of resolution, and adding more data should help to address this (Straub et al. 2014). Given the prevalence of hybridization and polyploidy in *Dryopteris* (Sessa et al. 2012c) and ferns generally (Lovis 1978), nuclear markers are particularly desirable as they will allow us to further explore conflict among gene histories: comparing topologies based on *pgiC* and *gapCp* for the North American *Dryopteris* taxa confirms that such conflict exists (Sessa et al. 2012b). Additional gene tree conflicts will likely be uncovered that may be attributable to ancient hybridization and/or polyploidy events, though incomplete lineage sorting, introgression, and chloroplast capture may also have contributed. There is less consensus in the literature on the prevalence of these phenomena, however, and we hope that future research will illuminate their extent in ferns. Similar uncertainties exist for other large and widespread fern genera in which hybridization and polyploidy are known to occur, such as *Asplenium* L. and *Polystichum* Roth. Both of these large genera include patterns of reticulate speciation that have been the focus of recent molecular studies, e.g. Schneider et al. (2012), Dyer et al. (2012), and Chang et al. (2013) on *Asplenium* and Perrie et al. (2003) on *Polystichum*. Schneider and colleagues' (2012) study of *Asplenium* using two low-copy nuclear markers plus ITS found conflict between the markers that they interpreted as evidence of ancient reticulation events. Little and Barrington (2003) reported that 44% of *Polystichum* species investigated cytologically had been found to be polyploid, with the majority of these suspected to be allopolyploids.

The implications of these issues for taxonomy and classification are profound, for all groups where polyploidy and hybridization occur. Plant researchers undertaking reclassifications in recent years have largely moved towards phylogeny-based taxonomic systems, often with supraspecific taxa redefined to reflect only well-supported clades. Examples in ferns include *Arthropteris* J. Sm. (Liu et al. 2013), *Christiopteris* Copel. (Schneider et al. 2008), *Elaphoglossum* Schott ex J. Sm. (Vasco et al. 2009; Lóriga et al. 2013), *Microgramma* C. Presl (Salino et al. 2008), *Asplenium* (Chang et al. 2013), and *Dryopteris* (Zhang 2012; Zhang and Zhang 2012). But which tree should a group's classification system be based on? The majority of these recent fern studies have relied solely on plastid phylogenies, but the prevalence of reticulate processes in ferns will likely lead to conflicts in classification systems based solely on maternal relationships (for evidence of maternal plastid inheritance in ferns, see Gastony and Yatskievych (1992) and Vogel et al. (1998)). Clearly, both plastid and nuclear phylogenies should be consulted whenever possible before reclassifications are undertaken, so that the maternal and paternal histories can

each inform assessment of relationships and monophyly. Until recently, plastid phylogenies were the only ones feasible for many groups, but the advent of next-generation sequencing has brought phylogenies based on multiple, unlinked nuclear markers within the reach of most researchers. However, such large-scale phylogenomic studies in ferns lag far behind those in other groups due to the lack of a completely sequenced reference genome – ferns are in fact the only major plant lineage without such a resource (Pryer et al. 2002; Sessa et al. 2014). Genomic resources for ferns do exist, however, including a genetic linkage map for the evo-devo model fern *Ceratopteris richardii* Brongn. (Nakazato et al. 2006), and transcriptome data for 70 + species available from the 1000 Plant Transcriptomes project (Wickett et al. 2014; <http://onekp.com>). This resource was recently used to develop primer sets for 20 + single and low-copy nuclear markers that amplify across ferns (Rothfels et al. 2013, 2015), and which can be used in future phylogenetic studies to investigate reticulate histories and hopefully inform classification decisions.

Historical biogeographic reconstructions of widespread groups of ferns are also lacking in the literature compared to similar studies in the flowering plants, and the paucity of such studies has made it difficult to test a long-held paradigm in fern biology. Pteridologists traditionally assumed that ferns' microscopic, dust-like spores will lead to ubiquitous long-distance dispersal, which should dominate patterns of historical biogeography in widely distributed groups (Tryon 1985; 1986). Recent studies in several groups, including *Dryopteris* (Sessa et al. 2012a), *Pteridium* Gled. ex Scop. (Der et al. 2009), *Nephrolepis* Schott (Hennequin et al. 2010), and the scaly tree ferns, Cyatheaceae Kaulfuss (Korall and Pryer 2013), have found evidence for a significant role of vicariance in determining modern fern distributions, but not all of these studies have utilized the most sophisticated methods currently available to perform these reconstructions (e.g. LaGrange (Ree and Smith 2008), BayArea (Landis et al. 2013), or BioGeoBEARS (Matzke 2013)). Furthermore, even the most recently developed of these methods still face a challenge in the form of reticulate taxa: none of the available methods can explicitly account for multi-labeled topologies in which hybrids or polyploids are represented by more than one tip. This is a significant limitation for studies of historical biogeography in groups with reticulate histories. For *Dryopteris* in particular, which has a nearly cosmopolitan distribution, an additional challenge to conducting a comprehensive historical biogeographical analysis is the nearly complete lack of sequence data from African taxa. African ferns have generally received much less attention than taxa in other regions, but several recent studies have tantalizingly revealed an important role for Africa in shaping modern distributions in several unrelated groups of ferns, including the scaly tree ferns (Korall and Pryer 2013), members of Polypodiaceae sensu Smith et al. (Smith et al. 2006; Janssen et al. 2007), and *Marsilea* L. (Nagalingum et al. 2007). Our ability to reconstruct historical patterns and to further clarify the respective roles of long-distance dispersal and vicariance will be greatly enhanced by comprehensive global sampling of widespread groups, including a focus on African taxa in many cases, and by encouraging further development of ancestral state reconstruction methods that incorporate reticulate histories.

Incorporating climatic data will also greatly enhance our understanding of distribution and diversification patterns

in ferns, as well as our ability to predict how species will respond to changing climates. Recent applications of bioclimatic data in studies of fern distributions and species composition have shown that variables related to water availability (such as humidity and precipitation) play a large role in determining fern species composition (Cardelús et al. 2006; Jones et al. 2007; de Gasper et al. 2013), and that species respond differently to drought and desiccation in ways likely to lead to differential survival and extinction following climate change (Saldaña et al. 2013; Testo and Watkins 2013). An increased focus on the gametophyte generation in recent years (Watkins et al. 2007a, b; Pittermann et al. 2013; Testo and Watkins 2013) has revealed that this stage of the life cycle may be key to determining establishment and survival of ferns, and recent work in *Dryopteris* (Sessa and Givnish 2014) suggests that sporophyte water relations and gametophyte physiology likely play a larger role in determining species distributions of eastern North American *Dryopteris* species than does sporophytic light response. Similar studies in other groups are urgently required to illuminate the links between sporophyte and gametophyte biology, distribution patterns, and response to changing climates. A connection between hybridization and/or polyploidy and improved physiological performance has also long been suggested and intensively studied in angiosperms, particularly in crop species (e.g. Levin 1983; Leitch and Leitch 2008; Maherali et al. 2009; Soltis et al. 2010; te Beest et al. 2011). Very few similar studies have been carried out in ferns, and these have reached conflicting results about whether there are significant correlations of phenotypic or ecological traits with hybridization or ploidy level (e.g. Sessa and Givnish 2014). The scarcity of such studies is surprising given the prevalence of these phenomena in ferns. Future work integrating ploidy, distribution, and physiology will contribute greatly to our understanding of historical speciation processes in ferns, and should allow us to begin predicting future prospects for ferns in the face of climate change.

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