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Celebrating David Barrington's Contributions to Fern and Lycophyte Research: Introduction to an American Fern Journal Special Issue

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During the Botany 2019 meeting in Tucson, Arizona, a large group of colleagues convened to celebrate the career achievements of Professor David Stanley Barrington with a colloquium titled "Reticulate evolution and biogeography in ferns and lycophytes – a colloquium honoring Dr. David Barrington." The colloquium was organized by myself, Michael Sundue, and Nikisha Patel, and featured talks by eleven researchers from nine institutions, nearly all of whom are early career researchers. The talks covered a diverse array of topics but were united in their shared focus on themes and approaches advanced by Dave over the course of a career that has spanned six decades.

Dave's career in botany started during his undergraduate studies at Bates College, where he was particularly inspired by Harold E. "Hal" Hackett, a young phycologist who joined the faculty shortly before Dave's freshman year. To complete research for a term paper, Hal suggested that Dave visit the Farlow Herbarium library at Harvard University, where Dave came into contact with his future Ph.D. advisor, Rolla Tryon. Following his graduation from Bates in 1970, Dave started his doctoral studies at Harvard, becoming a member of one of the leading groups of fern systematists of the time. His dissertation research focused on the taxonomy of the tree fern genus *Trichipteris* (Cyatheaceae) (Barrington, 1976; Barrington, 1978); studying this challenging, principally South American group would provide him with a solid foundation that he would build upon later in his career.

In 1974, Dave joined the faculty at the University of Vermont, where he has remained to this day. Shortly after taking this position, Dave shifted his research activities to the genus *Polystichum* (Dryopteridaceae), which has remained a constant focus in his lab since (*e.g.*, Barrington, 1985b; Barrington, 1986; Barrington, 1990; Barrington, 1992; Barrington, 1995; Little and Barrington, 2003; Barrington, 1993; Driscoll and Barrington, 2007; Barrington, 2012; McHenry and Barrington, 2014; Jorgensen and Barrington, 2017; Patel *et al.*, 2018). Key to Dave's long and active career has been his enthusiasm for applying contemporary techniques and approaches in pursuit of the principal goals of his research: resolving reticulate evolutionary histories and understanding plant biogeography. A sabbatical spent at Chris Haufler's lab at the University of Kansas in the spring of 1985 had a particularly transformative impact on Dave's career. The goal of that visit was to learn isozyme electrophoresis, a technique that by that time was widely used in angiosperms but was just gaining traction in the fern and lycophyte community as a powerful way to infer the relationships of taxa in groups with complex

histories of hybridization and polyploidy. At the time of this sabbatical, the Haufler Lab (then including Tom Ranker, Mike Windham, Charlie Werth, and Paul Wolf) was at the forefront of the isozyme revolution in ferns; research in the Barrington Lab would soon feature this powerful technique (Barrington, Haufler, and Werth, 1989; Barrington, 1990; Barrington, 2003; Driscoll, Gilman, and Barrington, 2003). Later years brought other approaches, including RFLPs (Stein and Barrington, 1990), AFLPs (Koenemann, Maisonpierre, and Barrington, 2011), and Sanger sequencing of both chloroplast (Driscoll and Barrington, 2007; McKeown, Sundue, and Barrington, 2012; McHenry, Sundue, and Barrington, 2013; McHenry and Barrington, 2014; Testo, Watkins, and Barrington, 2015; Morero *et al.*, 2019) and nuclear loci (Dragon and Barrington, 1990; Jorgensen and Barrington, 2017; Lyons, McHenry, and Barrington, 2017; Patel *et al.*, 2018).

With this ever-evolving repertoire of techniques, Dave has successfully led an active research program at the University of Vermont that has contributed significantly to our understanding of plant diversity, especially of ferns of North America, Central America, and East Asia. During his career, Dave has authored over 60 peer-reviewed publications, including 29 in the last ten years.

Even more impressive than the number of publications is the impact that these publications have had in shaping the future of our discipline. Dave's most-cited single-author paper (194 citations at the time of writing, according to Google Scholar) is a review article titled "Ecological and Historical Factors in Fern Biogeography," which was published in the *Journal of Biogeography* nearly thirty years ago (Barrington, 1993). This paper is remarkably successful in its goal of advancing our understanding of fern biogeography through the synthesis of a century of research across diverse disciplines, and examination of citation history shows that it has influenced important advancements in biogeography, in ferns and beyond (DeForest Safford, 1999; Crisp *et al.*, 2001; Kessler, 2001). Even considering the large body of literature it inspired, a close read of Barrington (1993) makes it clear that many of the important questions raised in that work (How common is hybridization in tropical ferns? How closely do montane habitat islands mirror patterns observed in oceanic island biogeography?) remain to be fully addressed, providing fertile ground for future generations of biogeographers.

Two other papers, each published in the *American Fern Journal* and with Dave as the lead author, stand out to me as being particularly influential contributions to the study of reticulate evolution in ferns and lycophytes. The first of these, "Systematic inferences from spore and stomate size in the ferns" by Barrington, Paris, and Ranker (1986) established that closely related ferns of different ploidy levels could, in most cases, be reliably distinguished by the size of their stomata and spores. This fast, low-cost, and effective approach has been a key part of the fern systematist's toolkit ever since, and has played an important role in resolving previously intractable polyploid complexes in genera like *Myriopteris* (Grusz, Windham, and Pryer, 2009), *Cystopteris* (Haufler and Windham, 1991; Rothfels *et al.*, 2014), *Polypodium* (Haufler

and Windham, 1991), and *Astrolepis* (Benham, 1992; Beck *et al*., 2010). Driven by an insatiable intellectual curiosity and a desire to see a good method become better, Dave, along with students Nikisha Patel and Morgan Southgate, recently revisited this topic, providing even more sophisticated insights into the relationship between spore size, ploidy level, and genome size in ferns (Barrington *et al*., 2020). The second, "Hybridization, reticulation, and species concepts in the ferns" by Barrington, Haufler, and Werth (1989), carefully examines how hybridization and polyploidy complicate the application of species concepts in ferns and provides thoughtful suggestions for how fern and lycophyte biologists can make sense of extant fern diversity (namely by recognizing evolutionary cohesive lineages of hybrid origin as species, in most cases). With its cogent responses to fundamental questions of evolutionary biology ("Are there two distinguishable kinds of species, hybrid species (nothospecies) and divergent species (orthospecies), as Wagner contends (1969, 1983)?"), this paper strikes me as even more important today than when I first read it as an undergraduate student, nearly a decade ago.

In addition to maintaining a productive research career, Dave has been an exceptional mentor to generations of students at the University of Vermont. He has advised 21 Master's and Ph.D. students and inspired hundreds of undergraduate students, especially participants in his tropical botany field course, which he has taught in Costa Rica every other year since 1979. For these exceptional efforts in teaching, he has received two awards at the University of Vermont: the Joseph E. Carrigan Award for Excellence in Undergraduate Teaching and the Kroepsch-Maurice Outstanding Teacher Award. As a former student of Dave's who had the good fortune to take several of his courses during graduate school, I strive to emulate his enthusiasm and success in inspiring students in my own classes.

As I reflect on Dave's successful career, I would be remiss if I failed to acknowledge the important role of his longtime collaborator and partner of more than 35 years, Cathy Paris. In addition to co-authoring several papers with Dave (Barrington, Paris, and Ranker, 1986; Barrington and Paris, 2007), Cathy has made several other important contributions to fern biology, especially on systematics of the maidenhair ferns (*Adiantum*) (Paris and Windham, 1988; Paris, 1991). As he has attested to in the acknowledgments of dozens of publications, Dave has benefitted tremendously from scientific conversations and editorial advice from Cathy, who is both an accomplished systematist and talented editor. Put simply, it would be hard to overstate the extent to which Cathy has helped make Dave the exceptional botanist, teacher, and mentor that he is.

Circling back to the colloquium mentioned in the beginning of this piece, a glance at that event's lineup of speakers highlights Dave's success in inspiring future generations of fern and lycophyte biologists: seven of the talks were presented by current or former Barrington Lab members, and all the talks focused on themes advanced by Dave during his career. Following an introduction by the colloquium organizers, the session included eleven talks, which are listed below:

1. "David Barrington: fern fanatic, consummate collector, creative collaborator, and *Polystichum* whisperer par excellence" -Christopher Haufler
2. Persistence pays off: long term field work in the Rockies yields another species of reticulate origin in the Moonwort Complex" -Arthur Gilman, Steve Popovich, and Don Farrar
3. "Ecological outcome of allopolyploidy in *Adiantum* (Pteridaceae): niche intermediacy and expansion into novel habitats" -Morgan Southgate, David Barrington, and Nikisha Patel
4. "Long-distance dispersal and geographical range expansions of the polyploid lineages in *Deparia* ferns (Athyriaceae; Polypodiales)" -Li-Yaung Kuo
5. "Species boundaries and population structure in the pan-tropical fern genus *Ceratopteris* (Pteridaceae)" -Sylvia Kinosian and Paul Wolf
6. "Ten years later: revisiting the *Myriopteris yavapensis* complex (Pteridaceae) in the genomics era" -Amanda Grusz
7. "600-species phylogenomic dataset provides insights into historical global biogeography of the Thelypteridaceae, with special reference to Hawaiian and African taxa" – Susan Fawcett, David Barrington, Michael Sundue, Gordon Burleigh, Emily Sessa, GoFlag consortium, Li Yaung Kuo, and Alan Smith
8. "Global patterns of fern diversification" -Jacob Suissa
9. "Polyploid speciation in the *Polystichum* of the Sierra Talamanca" -Stacy Jorgensen
10. "Reticulate evolutionary histories of the apomictic lineages in East Asian *Polystichum*" -Nikisha Patel
11. "Fifty years of fern hybridization and historical biogeography: new perceptions and new tools, all addressing the same fundamental questions" -David Barrington

This special issue of the American Fern Journal builds on this colloquium and includes six papers that explore diverse topics ranging from resolving reticulate complexes to Neotropical fern biogeography. The series begins with two studies focused on polyploid complexes. In the first, Jorgensen and Barrington (151–164) use nuclear DNA sequence data to provide new perspectives on the evolution of Central American *Polystichum*, a group that has been a main focus of Dave's research for more than 35 years. In the second, Popovich, Farrar, and Gilman (165–182) describe a new allotetraploid *Botrychium* from western North America based on combined datasets of allozymes and detailed morphological measurements. Following these, Fawcett (183–192) describes a new species of *Goniopteris* (Thelypteridaceae) known only from a single location in southwestern Dominican Republic. The fourth contribution is by Kinosian, Pearse, and Wolf (193–210), who use a RADseq approach to highlight widespread hybridization in *Ceratopteris* (Pteridaceae) and possible undescribed lineages. The fifth paper in the issue by Suissa and Sundue (211–232) uses a large specimen-based dataset and a phylogenetic framework to revisit classic hypotheses of Neotropical fern

biogeography proposed by Rolla Tryon nearly a half-century ago (Tryon, 1972). In the issue's final contribution, Barrington (233–254) presents a review of biogeography of polyploid ferns, focusing on six groups of ferns that he and his students studied extensively over the last four decades.

Together, the articles in this issue highlight the extent to which David Barrington's contributions have influenced a generation of innovative and active fern and lycophyte biologists and helped usher in a new and exciting era of discovery. I hope that readers of this special issue will enjoy reading these articles as much as I have enjoyed working with them through the editorial process.

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