

WILLIAM (NED) FRIEDMAN

CURRICULUM VITAE

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ADDRESS

Department of Organismic and Evolutionary Biology *and* Arnold Arboretum
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EDUCATION

Ph.D. in Botany (1986), University of California, Berkeley
A.B. in Biology (1981), Oberlin College

PROFESSIONAL EXPERIENCE

Director of the Arnold Arboretum of Harvard University (2011-)
Arnold Professor of Organismic and Evolutionary Biology, Harvard University (2011-)
Faculty Associate, Harvard University Center for the Environment (2011-)
Professor of Biology, University of Colorado (1999-2010)
Associate Professor of Biology, University of Colorado (1995-1999)
Associate Professor of Botany, University of Georgia (1993-1995)
Assistant Professor of Botany, University of Georgia (1987-1993)
Adjunct Faculty, Complex Carbohydrate Research Center, University of Georgia (1988-1995)
Adjunct Faculty, Warnell School of Forest Resources, University of Georgia (1992-1995)
Member, Center for Plant Cellular and Molecular Biology, University of Georgia (1987-1995)
Member, Institute of Ecology, University of Georgia (1991-1995)
Postdoctoral Research Associate, University of Arizona (1986-1987)

PROFESSIONAL FELLOWSHIPS, AWARDS & HONORS

Member of the Horticultural Club of Boston (by election, 2015-present)
Member of the Examiner Club of Boston (by election, 2014-present)
Fellow of the American Association for the Advancement of Science (2011-present)
Pelton Award, Botanical Society of America (for sustained and imaginative contributions in the field of plant developmental biology, 2004)
Waynflete Lectures, University of Oxford (by election, 1999)
Visiting Fellowship, Magdalen College, University of Oxford (by election, 1999)
Fellow of the Linnean Society (London) (1995-present)
Creative Research Medal, University of Georgia (1993)
Presidential Young Investigator Award, National Science Foundation (1991)
Faculty Research Award, Sigma Xi, The Scientific Research Society, University of Georgia Chapter (1991)

PROFESSIONAL FELLOWSHIPS, AWARDS & HONORS (cont.)

Lilly Teaching Fellow, University of Georgia (1988)
Sigma Xi, Full Membership, University of Georgia (1988); Associate Membership, Oberlin College (1981)
National Science Foundation Graduate Student Fellowship (1982)
University of California Regents Fellowship (1981)
Phi Beta Kappa, Oberlin College (1981)
Graduation with High Honors in Biology, Oberlin College (1981)

RESEARCH INTERESTS

Origin and early evolution of flowering plant reproduction (double fertilization/endosperm)
Evolution of naked buds in temperate woody plants
Intellectual history of early evolutionism and plant morphology
Role of heterochrony in the evolution of plant developmental patterns
Evolution of structural complexity and symbioses in early land plants
Patterns of cell cycle expression associated with gametogenesis and fertilization in plants

PROFESSIONAL GRANTS – AWARDED

National Science Foundation, Division of Environmental Biology, Research Coordination Network Program, “microMORPH, Microevolutionary Molecular and Organismic Research in Plant History” (\$481,736; Principal Investigator; 2010-2017)

National Science Foundation, Division of Integrative Organismal Systems, Developmental Systems Cluster, “Did the first angiosperms lack an embryo-nourishing endosperm?” (\$500,000; sole Principal Investigator; 2009-2013)

National Science Foundation, Division of Integrative Biology and Neuroscience, Ecological and Evolutionary Physiology Program, “Developmental evolution of fertilization biology in ancient angiosperm lineages” (\$499,585; sole Principal Investigator; 2005-2009)

NASA Astrobiology Initiative, “University of Colorado Center for Astrobiology – Origin of complex land-based ecosystems” (total award \$5,000,000; individual award \$244,000; co-Investigator; 2004-2009)

National Science Foundation, Division of Biological Instrumentation, Research Coordination Network Program, “MORPH, Molecular and Organismic Research in Plant History” (\$498,128; sole Principal Investigator; 2003-2010)

National Science Foundation, Division of Integrative Biology and Neuroscience, Extension for Special Creativity (CREX) to continue studies of “The evolution of double fertilization and endosperm development in basal flowering plants” (\$160,000; sole Principal Investigator; 2002-2004)

National Science Foundation, Major Research Instrumentation Program, “Acquisition of a confocal microscope and the establishment of an interdepartmental microscopy imaging facility at the University of Colorado” (\$306,920, with additional \$131,538 match from the University of Colorado; one of three co-Investigators; 2002-2005)

PROFESSIONAL GRANTS - AWARDED (cont.)

National Science Foundation, Ecological and Evolutionary Physiology Panel, "Evolution of double fertilization and endosperm development in basal flowering plants" (\$273,000; sole Principal Investigator; 1999-2002)

NASA Astrobiology Initiative, "University of Colorado Center for Astrobiology - Early evolution of terrestrial photosynthetic life and multicellularity" (total award \$2,800,000; individual award \$207,000; co-Investigator; 1998-2003)

National Science Foundation, Presidential Young Investigator Award, "The evolution of double fertilization and endosperm" (\$404,000; sole Principal Investigator; 1991-1998)

Interagency - Plant Biology (DOE/NSF/USDA), "Interdisciplinary research training group on mechanisms of plant evolution" (\$1,400,000; Faculty Participant, University of Georgia; 1992-1995)

National Science Foundation, Academic Research Infrastructure, "Acquisition of a Zeiss CEM902 spectroscopic transmission electron microscope" (\$134,013; Major User; 1992)

National Science Foundation, Instrumentation and Instrument Development, "High pressure freezer for advanced electron microscopy" (\$77,305; Major User; 1992)

National Science Foundation, Biotic Systems and Resources, Systematics Panel, "Sexual reproduction in *Ephedra* and its bearing on the evolution of double fertilization and endosperm in angiosperms" (\$155,990; sole Principal Investigator; 1988-1991)

National Science Foundation Graduate Fellowship (three years tuition and stipend; 1982-1984, 1985-1986)

University of California Regents Fellowship (one year tuition and stipend; 1981-1982)

PUBLICATIONS

Schoonderwoerd, K. and **W.E. Friedman**. 2016. Zygotic dormancy underlies prolonged seed development in *Franklinia alatamaha* (Theaceae): a most unusual case of reproductive phenology in angiosperms. *Botanical Journal of the Linnean Society* 181: 70-83.

Pirone-Davies, C., N. Prior, P. von Aderkas, D. Smith, D. Hardie, **W.E. Friedman**, and S. Mathews. 2016. Insights from the pollination drop proteome and the ovule transcriptome of *Cephalotaxus* at the time of pollination drop production. *Annals of Botany* 117: 973-984.

Friedman, W.E., M.S. Dosmann, T.M. Boland, D.E. Boufford, M.J. Donoghue, A. Gapinski, L. Hufford, P.W. Meyer and D.H. Pfister. 2016. Developing an exemplary collection: a vision for the next century at the Arnold Arboretum of Harvard University. *Arnoldia* 73(3): 2-18.

Friedman, W.E. 2015. Development and evolution of the female gametophyte and fertilization process in *Welwitschia mirabilis*. *American Journal of Botany* 102: 312-324.

Friedman, W.E. 2015. Evolving words and the egg-bearing tubes of *Welwitschia*. *American Journal of Botany* 102: 176-179.

PUBLICATIONS (cont.)

- Leff, J.W., P. Del Tredici, **W.E. Friedman** and N. Fierer. 2015. Spatial structuring of bacterial communities within individual *Ginkgo biloba* trees. *Environmental Microbiology* 17: 2352-2361.
- Povilus, R.A., J. M. Losada and **W.E. Friedman**. 2015. Floral biology and ovule and seed ontogeny of *Nymphaea thermarum*, an autogamous water lily at the brink of extinction with potential as a model system for basal angiosperms. *Annals of Botany* 115: 211-226.
- Losada, J.M., M. Herrero, J.I. Hormaza and **W.E. Friedman**. 2014. Arabinogalactan proteins mark stigmatic receptivity in the protogynous flowers of *Magnolia virginiana* (Magnoliaceae). *American Journal of Botany* 101: 1963-1975.
- Friedman, W.E.** and J.B. Bachelier. 2013. Seed development in *Trimenia* (Trimeniaceae) and its bearing on the evolution of embryo-nourishing strategies in early flowering plant lineages. *American Journal of Botany* 100: 906-915.
- Friedman, W.E.** 2013. One genome, two ontogenies. *Science* 339: 1045-1046 (invited perspective).
- Friedman, W.E.** 2013. Mutants in our midst. *Arnoldia* 71 (1): 2-14.
- Wu, C.C., P.K. Diggle and **W.E. Friedman**. 2013. Kin recognition within a seed and the effect of genetic relatedness of an endosperm to its compatriot embryo on maize seed development. *Proceedings of the National Academy of Sciences* 110: 2217-2222.
- Friedman, W.E.**, J.B. Bachelier and J.I. Hormaza. 2012. Embryology in *Trithuria submersa* (Hydatellaceae) and relationships between embryo, endosperm, and perisperm in early-diverging flowering plants. *American Journal of Botany* 99: 1083-1095.
- Ishikawa, M., T. Murata, Y. Sato, T. Nishiyama, Y. Hiwatashi, A. Imai, M. Kimura, N. Sugimoto, A. Akita, Y. Oguri, **W.E. Friedman**, M. Hasebe and M. Kubo. 2011. *Physcomitrella* cyclin-dependent kinase A links cell cycle reactivation to other cellular changes during reprogramming of leaf cells. *Plant Cell* 23: 2924-2938.
- Bachelier, J.B. and **W.E. Friedman**. 2011. Female gamete competition in an ancient angiosperm lineage. *Proceedings of the National Academy of Sciences* 108: 12360-12365.
- Friedman, W.E.** 2011. Plant genomics: Homoplasy heaven in a lycophyte genome. *Current Biology* 21: 554-556.
- Friedman, W.E.** and P.K. Diggle. 2011. Charles Darwin and the origins of plant evolutionary developmental biology. *Plant Cell* 23: 1194-1207
- Wu, C.-C., P.K. Diggle and **W.E. Friedman**. 2011. Female gametophyte development and double fertilization in Balsas teosinte, *Zea mays* subsp. *parviglumis* (Poaceae). *Sexual Plant Reproduction* 24: 219-229.
- Madrid, E.N. and **W.E. Friedman**. 2010. Female gametophyte and early seed development in *Peperomia* (Piperaceae). *American Journal of Botany* 97: 1-14.

PUBLICATIONS (cont.)

Friedman, W.E. 2009. Evolution pioneers: celebrating Lamarck at 200, Darwin 215. *Nature* 461: 167 (correspondence).

Friedman, W.E. 2009. Auxin at the evo-devo intersection. *Science* 324: 1652-1653 (invited perspective).

Winther, J.L. and **W.E. Friedman**. 2009. Phylogenetic affinity of arbuscular mycorrhizal symbionts in *Psilotum nudum*. *Journal of Plant Research* 122: 485-496.

Madrid, E.N. and **W.E. Friedman**. 2009. The developmental basis of an evolutionary diversification of female gametophyte structure in *Piper* and Piperaceae. *Annals of Botany* 103: 869-884.

Friedman, W.E. and K.C. Ryerson. 2009. Reconstructing the ancestral female gametophyte of angiosperms: insights from *Amborella* and other ancient lineages of flowering plants. *American Journal of Botany* 96: 129-143.

Friedman, W.E. 2009. The meaning of Darwin's "abominable mystery." *American Journal of Botany* 96: 5-21.

Holloway, S.J. and **W.E. Friedman**. 2008. Embryological features of *Tofieldia glutinosa* and their bearing on the early diversification of monocotyledonous plants. *Annals of Botany* 102: 167-182.

Friedman, W.E., S.C.H. Barrett, P.K. Diggle, V.F. Irish and L. Hufford. 2008. Whither plant evo-devo? Investigating the evolution of plant form: conceptual integration from the molecular to the ecological. *New Phytologist* 178: 468-471.

Friedman, W.E. 2008. Hydatellaceae are water lilies with gymnospermous tendencies. *Nature* 453: 94-97. (Faculty of 1000, Factor = 6.4, "Must Read").

Madrid, E.N. and **W.E. Friedman**. 2008. Female gametophyte development in *Aristolochia labiata* Willd. (Aristolochiaceae). *Botanical Journal of the Linnean Society*, 158: 19-29.

Friedman, W.E., E.N. Madrid and J.H. Williams. 2008. Origin of the fittest and survival of the fittest: relating female gametophyte development to endosperm genetics. *International Journal of Plant Sciences* 169: 79-92.

Winther, J.L. and **W.E. Friedman**. 2008. Arbuscular mycorrhizal associations in *Huperzia* and *Lycopodium* (Lycopodiaceae). *New Phytologist* 177: 790-801.

Winther, J.L. and **W.E. Friedman**. 2007. Arbuscular mycorrhizal associations in *Botrychium*. *American Journal of Botany* 94: 1248-1255.

Friedman, W.E. 2006. Sex among the flowers. *Natural History* 115 (9): 48-53.

Friedman, W.E. 2006. Embryological evidence for developmental lability during early angiosperm evolution. *Nature* 441: 337-340. (Faculty of 1000, Factor = 6.4, "Must Read").

PUBLICATIONS (cont.)

Friedman, W.E., R.C. Moore and M.D. Purugganan. 2004. The evolution of plant development. *American Journal of Botany* 91: 1726-1741.

Friedman, W.E. and J.H. Williams. 2004. Developmental evolution of the sexual process in ancient flowering plant lineages. *Plant Cell* (supplement) 16: 119-132.

Williams, J.H. and **W.E. Friedman**. 2004. The four-celled female gametophyte of *Illicium* (Illiciaceae; Austrobaileyales) and its implications for the origin and early evolution of monocots, eudicots and eumagnoliids. *American Journal of Botany* 91:332-351.

Friedman, W.E., W.N. Gallup and J.H. Williams. 2003. Female gametophyte development in *Kadsura*: implications for Schisandraceae, Austrobaileyales, and the early evolution of flowering plants. *International Journal of Plant Sciences* 164 (5) (supplement): 293-305.

Friedman, W.E. and J.H. Williams*. 2003. Modularity of the angiosperm female gametophyte and its bearing on the early evolution of endosperm in flowering plants. *Evolution* 57: 216–230. (*equal authorship).

Williams, J.H. and **W.E. Friedman***. 2002. Identification of diploid endosperm in an early angiosperm lineage. *Nature* 415: 522-526. (*equal authorship). (Faculty of 1000, Factor = 9.6, “Exceptional”).

Hiscock, S.J., K. Hoedemaekers, **W.E. Friedman** and H.G. Dickinson. 2002. The stigma surface and pollen-stigma interactions in *Senecio squalidus* L. (Asteraceae) following cross (compatible) and self (incompatible) pollinations. *International Journal of Plant Sciences* 163: 1-16.

Floyd, S.K. and **W.E. Friedman**. 2001. Developmental evolution of endosperm in basal angiosperms: evidence from *Amborella* (Amborellaceae), *Nuphar* (Nymphaeaceae), and *Illicium* (Illiciaceae). *Plant Systematics and Evolution* 228: 153-169.

Friedman, W.E. 2001. Comparative embryology of basal angiosperms. *Current Opinion in Plant Biology* 4: 14-20.

Friedman, W.E. 2001. Developmental and evolutionary hypotheses for the origin of double fertilization and endosperm. *Comptes Rendus de l'Academie des Sciences (Paris), Sciences de la vie* 324:559-567.

Friedman, W.E. and S.K. Floyd. 2001. The origin of flowering plants and their reproductive biology: a tale of two phylogenies. *Evolution* 55: 217-231.

Floyd, S.K. and **W.E. Friedman**. 2000. Evolution of endosperm developmental patterns among basal flowering plants. *International Journal of Plant Sciences* 161 (6) (supplement): 57-81.

Friedman, W.E. and M.E. Cook. 2000. The origin and early evolution of tracheids in vascular plants: integration of paleobotanical and neobotanical data. *Philosophical Transactions of the Royal Society London B* 355: 857-868.

PUBLICATIONS (cont.)

Williams, J.H., **W.E. Friedman** and M.L. Arnold. 1999. Developmental selection within the angiosperm style: using gamete DNA to visualize interspecific pollen competition. *Proceedings of the National Academy of Sciences* 96: 9201-9206.

Floyd, S.K., V.T. Lerner and **W.E. Friedman**. 1999. Developmental embryology of *Platanus* (Platanaceae), a basal eudicot. *American Journal of Botany* 86: 1523-1537.

Friedman, W.E. 1999. Expression of the cell cycle in sperm of *Arabidopsis thaliana*: implications for understanding patterns of gametogenesis and fertilization in flowering plants. *Development* 126: 1065-1075.

Cook, M.E. and **W.E. Friedman**. 1998. Tracheid structure in a primitive extant plant provides an evolutionary link to earliest fossil tracheids. *International Journal of Plant Sciences* 159: 881-890

Friedman, W.E. and J.S. Carmichael. 1998. Heterochrony and developmental innovation: evolution of female gametophyte ontogeny in *Gnetum*, a highly apomorphic seed plant. *Evolution* 52: 1016-1030.

Friedman, W.E. 1998. The evolution of double fertilization and endosperm: an "historical" perspective. *Sexual Plant Reproduction* 11: 6-16.

Friedman, W.E. and E.M. Gifford. 1997. Development of the male gametophyte of *Ginkgo biloba*: a window into the reproductive biology of early seed plants. *In: Botanical Society of Japan Special Volume, Ginkgo biloba*. T. Hori, ed. Springer Verlag, Tokyo, pp. 29-49.

Friedman, W.E. 1996. Introduction to biology and evolution of the Gnetales. *International Journal of Plant Sciences* 157(6) (supplement): 1-2. (Publication not peer reviewed).

Friedman, W.E. and J.S. Carmichael. 1996. Evolution of fertilization patterns in Gnetales: implications for understanding reproductive diversification among anthophytes. *International Journal of Plant Sciences* 157 (6) (supplement): 77-94.

Carmichael, J.S. and **W.E. Friedman**. 1996. Double fertilization in *Gnetum gnemon*, (Gnetaceae): its bearing on the evolution of sexual reproduction within the Gnetales and the anthophyte clade. *American Journal of Botany* 83: 767-780.

Carmichael, J.S. and **W.E. Friedman**. 1995. Double fertilization in *Gnetum gnemon*, a nonflowering seed plant: the relationship between the cell cycle and sexual reproduction. *Plant Cell* 7: 1975-1988.

Friedman, W.E. 1995. Organismal duplication, inclusive fitness theory and altruism: understanding the evolution of endosperm and the angiosperm reproductive syndrome. *Proceedings of the National Academy of Sciences* 92: 3913-3917.

Friedman, W.E. 1994. The evolution of embryogeny in seed plants and the developmental origin and early history of endosperm. *American Journal of Botany* 81: 1468-1486.

Liu, L., J.F.D. Dean, **W.E. Friedman** and K.-E.L. Eriksson. 1994. A laccase-like phenoloxidase is correlated with lignin biosynthesis in *Zinnia elegans* stem tissues. *Plant Journal* 6: 213-224.

PUBLICATIONS (cont.)

Friedman, W.E. 1993. The evolutionary history of the seed plant male gametophyte. *Trends in Ecology and Evolution* 8: 15-21.

Friedman, W.E. 1992. Double fertilization in nonflowering seed plants. *International Review of Cytology* 140: 319-355.

Crook, R.W. and **W.E. Friedman**. 1992. Effects of pollen number and archegonial number on fertilization in Douglas fir: significance for seed orchard management. *Canadian Journal of Forest Research* 22: 1483-1488.

Friedman, W.E. 1992. Evidence of a pre-angiosperm origin of endosperm: implications for the evolution of flowering plants. *Science* 255: 336-339.

Friedman, W.E. 1991. Double fertilization in *Ephedra trifurca*, a non-flowering seed plant: the relationship between fertilization events and the cell cycle. *Protoplasma* 165: 106-120.

Choi, J.S. and **W.E. Friedman**. 1991. Development of the pollen tube in *Zamia furfuracea* and its evolutionary implications. *American Journal of Botany* 78: 544-560.

Holaway, B.L., M.C. Trull, **W.E. Friedman** and R.L. Malmberg. 1991. A developmentally regulated antigen associated with calcium oxalate and calcium phosphate crystals in tobacco anthers. *Planta* 186: 13-16.

Friedman, W.E. 1990. Sexual reproduction in *Ephedra nevadensis* (Ephedraceae): further evidence of double fertilization in a nonflowering seed plant. *American Journal of Botany* 77: 1582-1598.

Friedman, W.E. 1990. Double fertilization in *Ephedra nevadensis*, a nonflowering seed plant: its bearing on the origin of angiosperms. *Science* 247: 951-954.

Friedman, W.E. and E.M. Gifford. 1988. Division of the generative cell and late development of the male gametophyte of *Ginkgo biloba*. *American Journal of Botany* 75: 1434-1442.

Friedman, W.E. 1987. Morphogenesis and experimental aspects of growth and development of the male gametophyte of *Ginkgo biloba* in vitro. *American Journal of Botany* 74: 1816-1830.

Friedman, W.E. 1987. Growth and development of the male gametophyte of *Ginkgo biloba* within the ovule (in vivo). *American Journal of Botany* 74: 1797-1815.

Friedman, W.E. and T.E. Goliber. 1986. Photosynthesis in the female gametophyte of *Ginkgo biloba*. *American Journal of Botany* 73: 1261-1266.

Robichaux, R.H., P.W. Rundel, W.L. Stemmermann, J.E. Canfield. S.R. Morse and **W.E. Friedman**. 1984. Tissue water deficits and plant growth in wet tropical environments. In: *Physiological Ecology of Plants of the Wet Tropics*. H.A. Mooney, E. Medina, and C. Vasquez-Yaney (eds.). Junk Publishers, The Hague, pp. 99-112.

Benzing, D.H., D.W. Ott, and **W.E. Friedman**. 1982. Roots of *Sobralia macrantha* (Orchidaceae): structure and function of the velamen-exodermis complex. *American Journal of Botany* 69: 608-614.

PUBLICATIONS (cont.)

Benzing, D.H., **W.E. Friedman**, G. Peterson, and A. Renfrow. 1983. Shootlessness, velamentous roots, and the pre-eminence of Orchidaceae in the epiphytic biotope. *American Journal of Botany* 70: 121-133.

Benzing, D.H. and **W.E. Friedman**. 1981. Mycotrophy: its occurrence and possible significance among epiphytic Orchidaceae. *Selbyana* 5: 243-247.

Benzing, D.H. and **W.E. Friedman**. 1981. Patterns of foliar pigmentation in Bromeliaceae and their adaptive significance. *Selbyana* 5: 224-240.

EDITED VOLUME

Friedman, W.E. 1996. Biology and evolution of the Gnetales. *International Journal of Plant Sciences* 157 (6): S1-S125.

INVITED SYMPOSIUM PRESENTATIONS

Symposium on Colonization of the Terrestrial Environment, 38th New Phytologist Symposium (Bristol UK, 2016). The texture of plant evolutionary history: how iterative and unique "events" shape biodiversity. Keynote speaker.

Symposium on Mutants in our Midst: Promoting Evolutionary Thinking in Horticultural and Botanical Living Collections, American Public Gardens Association (Denver, 2014). Organizer and speaker.

Symposium on the Life of Sir John Lubbock, Royal Society (London, 2013). The botanical contributions of John Lubbock, the last of the amateur naturalists.

Annals of Botany Annual Lecture, Botanical Society of America (Columbus, Ohio, 2012). Darwin's "abominable mystery" and the search for the earliest flowering plants.

Symposium on Bringing Biological Parts and Wholes into Historical and Philosophical Perspective, Chemical Heritage Foundation (Philadelphia, 2012). The history of plant modularity: from typological to developmental and evolutionary perspectives.

Student Conference on Evo-Devo, Weizmann Institute of Science (Rehovot, Israel, 2012). Charles Darwin and the origins of plant evolutionary-developmental biology.

Symposium on the Evolution and Development of the Angiosperm Female Gametophyte, International Botanical Congress (Melbourne, Australia, 2011). Organizer.

Symposium on the Reproductive Biology of Fruit Species, 28th International Horticultural Congress (Lisbon, Portugal, 2010). An evolutionary-developmental perspective on the angiosperm reproductive syndrome.

Symposium on the Evolution of Reproductive Development, International Association of Sexual Plant Reproduction Research (Bristol, United Kingdom, 2010). Plenary lecture. An evolutionary-developmental perspective on the angiosperm reproductive syndrome.

INVITED SYMPOSIUM PRESENTATIONS (cont.)

Symposium on Angiosperm Phylogeny and Biotic Evolution, 56th Annual Systematics Symposium, Missouri Botanical Garden (St. Louis, Missouri, 2009). Keynote Lecture. A Darwinian look at Darwin's evolutionist ancestors.

Symposium (Plenary Session) on the History of Developmental Biology, Society for Developmental Biology (San Francisco, 2009). From Goethe to MADS-box genes: Two centuries of botanical thought on homology and evolutionary developmental biology.

Symposium on Evolutionary Developmental Biology (Riverside, California, 2009). University of California, Riverside Biennial Plant Biology Symposium. Modularity and the evolutionary developmental basis of angiosperm reproduction.

Symposium on Evolution: Genomes, Cell Types and Shapes (Okazaki, Japan, 2008). National Institute of Basic Biology Japan and European Molecular Biology Laboratory. Modularity and the evolution of flowering plants.

Symposium on Frontiers in Sexual Plant Reproduction III (Tucson, Arizona, 2008). Overcoming a century of dogma about the reproductive features of the first angiosperms: insights from *Hydatella* and other water lilies.

Symposium on Plant Reproductive Systems: From the Molecular Basis of Reproductive Systems to Pollination Ecology. Zurich-Basel Plant Science Center (Zurich, 2007). Origin of the fittest and survival of the fittest: relating female gametophyte development to endosperm genetics.

Symposium on Evolutionary Development, American Society of Plant Biologists and Botanical Society of America (Chicago, 2007). An evolutionary-developmental perspective on the angiosperm reproductive syndrome.

Symposium on the Comparative Phylogenetic Method of Reconstructing Evolutionary History, Botanical Society of America (Chico, 2006). Assessing homology and interpreting developmental evolution within the complex life cycle of land plants.

Guild of Rocky Mountain Ecological and Evolutionary Biologists (2005). Evolution before Darwin: The making of Darwin's "Historical Sketch." Keynote address.

Jeanette Siron Pelton Award Lecture, Botanical Society of America (Austin, 2005). A generation forgotten and Goethe remembered: modularity and the evolution of flowering plants.

Symposium on Evolution and Function of Xylem Structure, International Botanical Congress (Vienna, 2005). The early evolution of water-conducting cells: integrating paleobotanical and neobotanical data.

Symposium on Origin and Early Evolution of Land Plants, International Botanical Congress (Vienna, 2005). Co-evolution of land plants and their mycorrhizal partners: implications for understanding the evolution of the alternation of generations. (coauthor, J. Winther presenting).

Symposium on Undergraduate Research, Society for the Study of Evolution (Fairbanks, 2005). MORPH, growing the next generation of plant evolutionary developmental biologists.

INVITED SYMPOSIUM PRESENTATIONS (cont.)

Symposium on Evolution and Development, Society for Developmental Biology Northwest Regional Conference (Friday Harbor Laboratories, 2005). Symposium Lecture: Modularity and the evolution of flowering plant reproductive patterns.

Symposium on Frontiers in Sexual Plant Reproduction II (Albany, New York, 2004). Modularity and the evolution of the female gametophyte in ancient angiosperms.

Ferns for the 21st Century Conference (Royal Botanic Gardens Edinburgh, 2004). The early evolution of mycorrhizal associations in land plants: a phylogenetic and evolutionary developmental perspective. (coauthor, J. Winther presenting).

Symposium on Discerning Homologies: Gene Expression, Development, and Morphology, Botanical Society of America (Snowbird, Utah, 2004). Co-organizer with Larry Hufford.

Symposium to Commemorate the Retirement of Donald Kaplan, Botanical Society of America (Snowbird, Utah, 2004). The botanical and evolutionist views of Erasmus Darwin (grandfather of Charles Darwin).

President's Plenary Symposium of the Botanical Society of America (Snowbird, Utah, 2004). Modularity and the evolution of the female gametophyte in ancient angiosperms.

Symposium on Structural and Functional Adaptations of Vascular Plants to Wetland Ecosystems, Botanical Society of America (Mobile 2003). Introduction and historical perspective.

Conference on Gametophytes, Evolution, Development and Function (Monte Verità, Ascona, Switzerland, 2003). Modularity and the evolution of the flowering plant female gametophyte.

Symposium on Flowers: Diversity, Development and Evolution (Institute of Systematic Botany, Zurich, 2002). Early evolution of the flowering plant reproductive syndrome.

Symposium on Plant Reproduction: From Evolutionary and Physiological Analyses to Molecular and Cellular Studies (Pennsylvania State University, 2002). Endosperm development and genetics in basal angiosperms: connecting the ontogenies of female gametophytes with endosperm evolution.

Symposium on Conifer Reproduction. Botanical Society of America and Canadian Botanical Association (Madison, Wisconsin, 2002). Mate choice in conifers: the dynamics of male-female interactions and phenotypic plasticity in female gametophyte development.

Guild of Rocky Mountain Population Biologists (Ghost Ranch Conference Center, 2001). The biology of early flowering plants: the continuing saga of Darwin's "abominable mystery." Keynote address.

Symposium on Frontiers in Sexual Plant Reproduction (Albany, New York, 2000). The cell cycle of plant gametes: timing is everything!

Symposium to Commemorate the Discovery of Double Fertilization, L'Académie des Sciences (Paris, 1999). Comparative and developmental insights into the evolutionary history of double fertilization in flowering plants.

INVITED SYMPOSIUM PRESENTATIONS (cont.)

Symposium on Endosperm Development, International Botanical Congress (St. Louis, 1999). The evolutionary origin of endosperm development and function.

Symposium on Newest Ideas on the Oldest Plants, International Botanical Congress (St. Louis, 1999). The evolutionary origin of water conducting cells in terrestrial plants (coauthor, M. Cook presenting).

Symposium on In Vivo and In Vitro Approaches to Understanding Double Fertilization in Flowering Plants, International Botanical Congress (St. Louis, 1999). Heterochrony and fertilization in seed plants (coauthor, J. Carmichael presenting).

Symposium on Molecular and Developmental Aspects of Basal Angiosperm Evolution, International Botanical Congress (St. Louis, 1999). Evolution of fertilization patterns and embryogeny among basal flowering plants (coauthor, S. Floyd presenting).

Symposium on Bryophyte Phylogeny and Interrelationships with Early Embryophytes, Royal Society (London, 1999). The evolutionary origin of water conducting cells in vascular plants, a developmental perspective.

Symposium on Heterochrony in Plants, Botanical Society of America (Baltimore, 1998). Heterochrony and developmental innovation during the evolution of seed plants.

Symposium on Plant Gametes and Fertilization, Botanical Society of America and Canadian Botanical Association (Montreal, 1997). Evolution of female gamete structure among seed plants.

Keystone Symposium on Evolution of Plant Development (Taos, New Mexico, 1997). Heterochrony and the evolution of reproductive systems of Gnetales and angiosperms.

Chicago Plant Science Symposium (Field Museum of Natural History, Chicago, 1996). The origin of flowering plants: an examination of Darwin's "abominable mystery"

Symposium on Use of Global Morphological Characters in Green Plant Phylogeny and Evolution, Botanical Society of America (Seattle, Washington, 1996). Evolutionary diversification of gametophyte structure and fertilization patterns among embryophytes.

Centenary Commemorative Symposium for the Discovery of *Ginkgo* Spermatozoids by Sakugoro Hirase (Tokyo Botanical Gardens, University of Tokyo, 1996). Development of the male gametophyte of *Ginkgo biloba*: a window into the reproductive biology of early seed plants.

Symposium on the Role of Plant Reproductive Biology in Systematics, Conservation and Economic Botany (The Royal Botanic Gardens, Kew, 1996). Keynote lecture.

14th International Congress of Sexual Plant Reproduction (Melbourne, 1996). Fertilization in the nonflowering seed plants *Ephedra* and *Gnetum*: implications for the evolution of double fertilization and endosperm.

Cold Spring Harbor Laboratory Conference on Plant Reproductive Biology (New York, 1996). Comparative and phylogenetic approaches to reconstructing the evolution of plant reproductive patterns.

INVITED SYMPOSIUM PRESENTATIONS (cont.)

Symposium on the Biology and Evolution of the Gnetales, Botanical Society of America (San Diego, California, 1995). The evolution of fertilization biology and embryo-nourishing patterns within the Gnetales: implications for understanding reproductive diversification within the anthophyte clade.

Symposium on the Evolution of Plant Architecture (The Royal Botanic Gardens, Kew, 1995). The role of architecture and exaptation in the evolution of key functional innovations of the seed plant male gametophyte.

Symposium on Fertilization in Seed Plants, International Botanical Congress (Japan, 1993). Double fertilization in nonflowering seed plants.

Symposium on Angiosperm Origin, Early Evolution and Phylogeny, Botanical Society of America (Ames, Iowa, 1993). Crossing the line: comparing female gametophyte structure, fertilization and endosperm development in primitive flowering plants and their outgroups.

Linnean Society Palynology Specialist Group (London, 1993). The evolutionary history of the seed plant male gametophyte.

Keystone Symposium on Evolution and Plant Development (Taos, New Mexico, 1993). Comparative and phylogenetic aspects of fertilization biology in seed plants: implications for understanding character evolution.

Symposium on Plant Development, Southeast Regional Developmental Biology Conference (Clemson, South Carolina, 1992). Double fertilization in *Ephedra*, a nonflowering seed plant: its bearing on the origin of angiosperms.

Symposium on Evolution and Development in Plants, Botanical Society of America (San Antonio, Texas, 1991). Comparative aspects of fertilization biology in seed plants: implications for reconstructing evolutionary history.

Symposium on Plant Gametes and Fertilization, Botanical Society of America (Richmond, Virginia, 1990). Double fertilization in nonflowering seed plants.

INVITED DEPARTMENTAL SEMINARS

2015: California Institute of Technology, Division of Biology and Biological Engineering; Wayne State University, Department of Biological Sciences; Wellesley College, Department of Biology; University of Toronto, Department of Botany; Bowdoin College, Department of Biology

2014: Humboldt State University, Department of Botany

INVITED DEPARTMENTAL SEMINARS (cont.)

- 2012: Purdue University, Department of Horticulture and Landscape Architecture; Denison University, Department of Biology; University of Massachusetts, Boston, Department of Biology; Cornell University, Department of Plant Biology; Connecticut College Departments of Biology and Botany; Peking University, Department of Biology; Chinese Academy of Sciences, Shanghai Chenshan Plant Science Research Center; Chinese Academy of Sciences, Institute of Botany (Beijing); Northwestern University, Graduate Program in Plant Biology and Conservation; University of Pennsylvania, Morris Arboretum; University of Georgia, Department of Genetics; University of Georgia, Department of Plant Biology; Real Jardín Botánico de Madrid; La Mayora Agricultural Research Station (Spain)
- 2011: Dartmouth College, Department of Biology; Tufts University, Department of Biology; Colby College, Department of Biology
- 2010: Harvard University, Department of Organismic and Evolutionary Biology; University of Tennessee, Department of Ecology and Evolutionary Biology; Harvard University, Harvard University Herbaria
- 2009: University of New England (Armidale, Australia), Department of Botany; University of Wyoming, Department of Botany; California State University, Northridge, Department of Biology; University of New Mexico, Department of Biology; University of California, Davis, Section of Plant Biology; University of Massachusetts, Department of Biology
- 2008: National Institute for Basic Biology (Okazaki, Japan); Salem College, Department of Biology; University of Missouri, Columbia, Division of Biological Sciences; Colorado College, Department of Biology
- 2007: Howard University, Department of Biology; Max Planck Institute for Plant Breeding Research (Cologne, Germany); Cornell University, Department of Plant Biology; Cornell University, Department of Ecology and Evolutionary Biology; American Museum of Natural History; Columbia University, Department of Ecology, Evolution, and Environmental Biology; University of Chicago, Department of Ecology and Evolution
- 2006: Oberlin College, Department of Biology; New York Botanical Garden; University of Georgia, Plant Biology Department; Yale University, Department of Ecology and Evolutionary Biology; Wesleyan University, Department of Biology; University of Connecticut, Department of Ecology and Evolutionary Biology; University of Washington, Department of Biology
- 2005: Western State College, Interdepartmental Seminar; University of Nebraska, Omaha, Department of Biology; Oberlin College, Interdepartmental Seminar; University of Denver, Department of Biology; University of Puerto Rico, Department of Biology
- 2004: University of Wyoming, Department of Botany; University of Maryland, Department of Biology; University of Missouri, St. Louis, Department of Biology; Western State College, Department of Biology; University of Munich, Herbarium and Botanical Gardens; University of Munich, Department of Evolutionary Biology; University of Zurich, Institute of Systematic Botany
- 2003: University of California, Davis, Plant Biology Graduate Group

INVITED DEPARTMENTAL SEMINARS (cont.)

- 2002: Harvard University, Department of Organismic and Evolutionary Biology; University of Toronto, Department of Botany; Colorado State University, Department of Biology; University of Michigan, Department of Ecology and Evolutionary Biology; University of Colorado, Denver, Department of Biology
- 2001: Michigan State University, Department of Plant Biology; Washington University, Department of Biology; University of Denver, Department of Biology; Pennsylvania State University, Department of Biology; University of Missouri, St. Louis, Department of Biology; University of Georgia, Department of Botany; Ohio State University, Department of Plant Biology; Washington State University, Institute of Biological Chemistry
- 2000: John Innes Centre (Norwich, England), Department of Genetics; Carleton College, Department of Biology; Oberlin College, Department of Biology; State University of New York, Binghamton, Department of Biology
- 1999: University of Victoria, Department of Biology; University of Northern Colorado, Department of Biology; Royal Botanic Gardens, Kew; University of Zurich, Institute of Systematic Botany; University of Oxford, Department of Plant Sciences; Max Plank Institute, Cologne; École Normale Supérieure de Lyon, Department of Plant Cell Biology; Lund University, Department of Ecology; University of Bath, Department of Biology; Natural History Museum, London; University of Vienna, Institute of Botany
- 1998: University of Chicago, Department of Molecular Genetics & Cellular Biology; Brigham Young University, Department of Botany; Duke University, Ecology and Evolutionary Biology Program; University of California, Berkeley, Museum of Paleontology; University of California Herbarium
- 1997: Pennsylvania State University, Plant Physiology Group; University of Zurich, Institute of Systematic Botany; University of Texas, Department of Botany; Southwest Texas State University, Department of Biology
- 1996: University of Tokyo, Biology Department; Colorado State University, Department of Biology
- 1995: Brown University, Department of Ecology and Evolutionary Biology; University of Oklahoma, Department of Botany and Microbiology; University of North Carolina, Greensboro, Department of Biology; University of Colorado, Department of EPO Biology; University of Minnesota, Department of Plant Biology
- 1994: University of Massachusetts, Department of Biology; University of Utah, Department of Biology; Smith College, Department of Biology; University of Arizona, Department of Ecology and Evolutionary Biology; University of New Mexico, Department of Biology; Washington State University, Department of Botany; University of Wyoming, Department of Botany; California Institute of Technology, Division of Biology; University of Denver, Department of Biological Sciences

INVITED DEPARTMENTAL SEMINARS (cont.)

- 1993: University of California, Berkeley, Department of Plant Biology; University of California, Davis, Department of Plant Sciences; University of North Carolina, Department of Biology; University of Kansas, Department of Systematics and Ecology; University of Oxford, Systematics Group; Agricultural University of Norway (Ås); University of Maryland, Department of Biology; University of Wisconsin, Department of Botany
- 1992: University of Missouri, Department of Biology; University of Colorado, Department of EPO Biology; Appalachian State University, Department of Biology; Arizona State University, Department of Botany and Microbiology; Northern Arizona University, Department of Biology; Ohio University, Department of Botany; University of Alberta, Department of Botany; Daytona Beach Community College, Department of Science
- 1991: Florida International University, Department of Biology; Louisiana State University, Department of Botany; Duke University, Department of Botany; North Carolina State University, Department of Botany; Westvaco Forestry Company, Research Department
- 1990: University of Minnesota, Duluth, Department of Biology; Oberlin College, Department of Biology; University of Connecticut, Department of Ecology and Evolutionary Biology; University of Arizona, Department of Plant Sciences; Indiana University, Department of Biology
- 1988: Auburn University, Department of Botany and Microbiology; University of Georgia, Complex Carbohydrate Research Center
- 1987: Pennsylvania State University, Department of Biology; Fairchild Tropical Garden (Research Facility); University of California, Davis, Department of Botany; University of Georgia, Department of Botany
- 1986: University of Arizona, Department of Plant Sciences

UNIVERSITY LECTURE SERIES

Waynflete Lectures, Magdalen College, University of Oxford (by election, 1999). Seminal events in the evolutionary history of plants (four lectures)

LECTURES TO THE GENERAL PUBLIC

Mutants in our midst: Darwin, horticulture, and evolution (Director's Lecture Series, Arnold Arboretum of Harvard University, 2014; Polly Hill Arboretum, 2015; Los Angeles County Arboretum and Botanical Garden, 2015)

Plants, the first three billion years: a reflection on the nature of evolutionary history (Director's Lecture Series, Arnold Arboretum of Harvard University, 2013)

Charles Darwin and the early evolutionists (Chicago Botanic Garden, 2012)

The evolution of big (Director's Lecture Series, Arnold Arboretum of Harvard University, 2013)

LECTURES TO THE GENERAL PUBLIC (cont.)

A Darwinian look at Darwin's evolutionist ancestors (Director's Lecture Series, Arnold Arboretum of Harvard University, 2011)

Darwin's "abominable mystery" and the search for the first flowering plants (Harvard Museum of Natural History, 2010)

Evolution before Darwin (Café Scientifique, Boulder, 2007, 2008)

Evolution before Darwin (Torrey Botanical Society Annual Lecture Series and New York Botanical Garden, 2006)

The evolutionary origin of flowering plants: an examination of Darwin's "abominable mystery" (Denver Museum of Nature and Science, 2005)

Evolution before Darwin (Denver Museum of Nature and Science, 2003)

The history of life on Earth: the impact of rare events (Denver Museum of Nature and Science, 2003)

Diversity of life on Earth: the second great age of discovery (Denver Museum of Nature and Science, Centennial Lecture Series, 2001) (Rocky Mountain Skeptics Club, 2002) (American Institute of Petroleum Geologists, Denver, 2002)

New views on the plants that took over the Cretaceous: the mysterious rise of flowering plants (Founders Symposium of the Western Interior Paleontological Society, Golden, Colorado, 2001)

The evolutionary history of plants: four billion years in four nights (Denver Museum of Natural History, 2000)

TEACHING EXPERIENCE

Sociobotany (Spring 2015, 2016)

Getting to Know Darwin, Freshman Seminar (Fall 2011-2015, Spring 2017)

Darwinian Revolution (Fall, 2009, 2010)

Plant Biodiversity and Evolution (Spring, 1996-1998; Fall, 1998; Spring, 2000-2005; Spring, 2008-2010)

Graduate Seminar, The Life of and Evolutionary Writings of Lamarck (Fall, 2008)

Graduate Seminar, The Life of Alfred Russel Wallace (Fall, 2007)

Graduate Seminar, Charles Lyell: Pre-Darwinian Evolutionist? (Fall, 2006)

Graduate Reading Group, Charles Darwin's Early Evolutionist Writings, 1837-1858 (Spring, 2005)

Graduate Reading Group, Darwin's Historical Sketch: Evolutionism's First Intellectual History (Spring, 2004)

Graduate Reading Group, The Life of Robert Chambers (Spring, 2003)

Graduate Reading Group, The Life of Alfred Russel Wallace (Spring, 2002)

Graduate Reading Group, The Life of Erasmus Darwin (Spring, 2001)

Plant Anatomy (Winter, 1988; Fall, 1988-1992, 1994-2002, 2006)

Graduate Seminar, Introduction to Graduate Research (Fall, 1999, 2000)

Evolutionary History of Land Plants (Winter, 1992)

TEACHING EXPERIENCE (cont.)

Graduate Seminar, The Origin and Early Evolution of Land Plants (Spring, 1995; Fall, 1996)
Graduate Seminar, The Biology of Epiphytes (Fall, 1995)
Graduate Seminar, Biology and Evolution of Conifers (Winter, 1994)
Graduate Seminar, The Origin and Early Evolution of Flowering Plants (Spring, 1993)
Graduate Seminar, The Evolutionary History of Land Plants (Winter, 1991)
Graduate Seminar, The Biology of Plant Meristems (Spring, 1990)
Graduate Seminar, Pollen and the Male Gametophyte (Spring, 1989)

THESES AND DISSERTATIONS DIRECTED

Kristel Schoonderwoerd (Ph.D. expected 2021), The evolution of bud morphology and ontogeny in Juglandaceae

Rebecca Ann Povilus (Ph.D. expected 2016), The evolutionary developmental basis of interparental conflict in flowering plant seeds

Chi-Chih Wu (Ph.D. 2012), Heterofertilization in maize: the effects of altered paternal relationships between endosperms and embryos

Eric Madrid (Ph.D. 2008), The evolution of female gametophyte development in Piperales

Jennifer Winther (Ph.D. 2007), Arbuscular mycorrhizal associations in mycoheterotrophic ferns and lycopods

Sandra Floyd (Ph.D. 2000), Evolution of endosperm development among basal angiosperms

Jeffrey Carmichael (Ph.D. 1995), Developmental and evolutionary aspects of fertilization in *Gnetum*, a nonflowering seed plant

Reed Crook (M.S. 1991), Pollen competition and female response to pollen quality in Douglas fir

Jung-Sung Choi (M.S. 1990), Cytological and ultrastructural studies of the growth of the pollen tube of *Zamia furfuracea* (Cycadales)

PROFESSIONAL COMMITTEES AND ACTIVITIES

Botanical Society of America, Development Committee (2016-present)
Botanical Society of America, Investment Committee (2015-present)
Botanical Society of America, Committee to Select New Editor of *American Journal of Botany* (2012-2013)
Botanical Society of America, Pelton Award Committee (2011-2014)
Editorial Board, *Sexual Plant Reproduction* (2011-2015)
International Prize for Biology (Japan), Selection Committee (2004, 2013)
Botanical Society of America, Publications Committee (2010-2013)
Associate Editor, *American Journal of Botany* (1995-1999; 2010-2015)
Editorial Committee, *Journal of Plant Research* (2006-2012)
Editorial Committee, *Biological Reviews* (2005-2010)
Editor, *International Journal of Plant Sciences* (1999-2015)

PROFESSIONAL COMMITTEES AND ACTIVITIES (cont.)

Botanical Society of America, Webpage Committee (2008-2009)
American Society of Plant Biologists, Early Career Award Committee (2008-2011)
Botanical Society of America, Committee on Committees (2006-2009; 2000-2002)
External Program Review, Oberlin College Biology Department (2005)
Associate Editor, *International Journal of Plant Sciences* (1998-1999)
Botanical Society of America, Committee to Select New Editor of *American Journal of Botany* (1998-1999)
External Program Review, University of Tennessee Botany Department (1998; Chair, 2002)
Botanical Society of America, Chair of the Developmental and Structural Section (1996-1998)
Botanical Society of America, Esau Student Award Committee (1996-1998; Chair, 1998)
Botanical Society of America, Representative to American Association for the Advancement of Science
Section on Biological Sciences (1994-1995)
Botanical Society of America, Committee to Select New Editor of *American Journal of Botany* (1993-1994)
Botanical Society of America, Structural and Developmental Section, Botany for the Next Millennium
Committee (1993)