

INTRODUCTION: EVOLUTION OF MODERN FERNS

Ruth A. Stockey and Gar W. Rothwell

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; and
Department of Environmental and Plant Biology, Ohio University, Athens, Ohio 45701, U.S.A.

The history of leptosporangiate fern systematics has been one of constant change, with the number of recognized living families ranging from nine to more than 40 (reviewed by Gifford and Foster [1989]) and additional extinct families that are preserved only in the fossil record (Stewart and Rothwell 1993; Taylor and Taylor 1993; Tidwell and Ash 1994). Recent advancements in our understanding of systematically informative structural characters and the advent of molecular systematics have allowed pteridologists to recognize grades and clades of ferns with increasing confidence (Hasebe et al. 1995; Pryer et al. 1995, 2004; Smith 1995; Rothwell 1999) and to more narrowly circumscribe families with living species (Kramer and Green 1990) that traditionally have been hard to identify from fossils. Accurate identification of many ferns requires data from a combination of external morphology, internal anatomy, epidermal appendages, phenology, karyotype analysis, chemical analyses, and molecular characters, and this entire combination is never preserved for a single species of fossils. Moreover, many structural characters of living ferns have not been extensively surveyed, so fragments of extinct fern species may be particularly difficult to identify and classify with confidence.

Two popular misconceptions about plant fossils tend to limit the impact of extinct species on evolutionary studies and to reduce the rate with which paleontological information is being incorporated into the mainstream of botanical knowledge. The first misconception is that the fossil record is already well sampled. From the global graveyard of sediments spread across the earth's surface, paleobotanists are constantly recovering unexpected new paleobotanical evidence. Indeed, the abundant new data presented in this single symposium demonstrate that much more information remains to be discovered. The second misconception is that the fossil record contains insufficient data for formulating and testing hypotheses about organismal diversity and patterns of plant phylogeny. By some estimates, as many as 99% of all the species that have inhabited the planet over geological time are now extinct (Novacek and Wheeler 1992), and in this regard fossil evidence may ultimately provide the greatest promise for developing an accurate picture of plant evolution and fern phylogeny. As plant paleontologists, we bear the responsibility to develop, publicize, and make available to the botanical community the valuable information and insights that are to be gleaned from evidence of past life. The compilation of studies that follows represents one attempt to do so.

Papers included in the special section of this issue of *International Journal of Plant Sciences* are derived primarily from a symposium titled "The Evolution of Modern Ferns," hosted by the Department of Biological Sciences, University of Al-

berta, in April 2004. Of the 13 contributions at that symposium, nine are included in this issue, along with four additional papers that could not be presented in the limited time available for the symposium talks. Twelve of the contributions present new data about fossil filicalean ferns that lived from the Upper Pennsylvanian to the Eocene, and several are supplemented by comparative data for closely related living species. These include a new family of Paleozoic Filicales (Tomescu et al. 2006) that represents the first (now entirely extinct) of three major leptosporangiate fern radiations (Rothwell 1987). The second major filicalean radiation (i.e., from the Permian to the Cretaceous) is represented by several new species of the Osmundaceae (Vavrek et al. 2006), Schizaeaceae (Hernandez-Castillo et al. 2006; Trivett et al. 2006), Gleicheniaceae (Mindell et al. 2006), Dipteridaceae (Stockey et al. 2006b), and Dennstaedtiaceae (Little et al. 2006). The third radiation of leptosporangiate ferns, which has produced most of the modern species richness since the Lower Cretaceous, is represented by studies of Thelypteridaceae (Stockey et al. 2006a), Athyriaceae (Karafit et al. 2006), Blechnaceae (Serbet and Rothwell 2006; Smith et al. 2006), Dryopteridaceae (Serbet and Rothwell 2006), and possibly Pteridaceae (Rothwell and Stockey 2006). The final paper of the special section (Rothwell and Nixon 2006) brings into focus our current understanding of the overall pattern of phylogeny for ferns as viewed from a paleontological perspective.

In addition to broadening our knowledge of diversity through descriptions of 13 new species, seven new genera, and one new family of filicalean ferns, these contributions expand our understanding of the structural diversity of ferns, provide intermediates between modern fern families, set new minimum ages for the origins of families and genera, refine concepts about the evolution of adaptive growth patterns, provide insights about ancient plant community structure and habitats of growth and fossil deposition, and elaborate the vital role that extinct species play in formulating robust hypotheses for patterns of phylogeny. We wish to stress that all the new paleobotanical data presented in this special section have been derived from only seven fossil localities in North America. Imagine how much new information remains to be developed from the untapped and underutilized Middle Devonian to Pleistocene plant fossil localities around the world!

We would like to dedicate this group of papers to our late friends Wes Wehr of the Burke Museum, University of Washington, and Alice Elizabeth (Betty) Speirs of Red Deer, Alberta. Wes was instrumental in setting up numerous collaborations between us and members of the Vancouver Island Paleontological Society that have provided much of the fossil data presented in these papers, and he is honored by the

description of a second species of the genus *Wessiea*, *Wessiea oroszii* Serbet and Rothwell (2006). Betty's tireless collecting for more than 25 years in central Alberta provided material

for studies of fossil mammals, insects, fish, and plants, one of which is here named in her honor, *Speirseopteris orbiculata* Stockey, Lantz et Rothwell (2006a).

Literature Cited

- Gifford EM, AS Foster 1989 Morphology and evolution of vascular plants. 3rd ed. Freeman, New York. 626 p.
- Hasebe M, PG Wolf, KM Pryer, K Ueda, M Ito, R Sano, G Gastony, et al 1995 Fern phylogeny based on *rbcL* nucleotide sequences. *Am Fern J* 85:134–181.
- Hernandez-Castillo GR, RA Stockey, GW Rothwell 2006 *Anemia quatsinoensis* sp. nov. (Schizaeaceae), a permineralized fern from the Lower Cretaceous of Vancouver Island. *Int J Plant Sci* 167:665–674.
- Karafit SJ, GW Rothwell, RA Stockey, H Nishida 2006 Evidence for sympodial vascular architecture in a filicalean fern rhizome: *Dickwhitea allenbyensis* gen. et sp. nov. (Athyriaceae). *Int J Plant Sci* 167:721–727.
- Kramer KU, PS Green 1990 Pteridophytes and gymnosperms. Vol 1 of The families and genera of vascular plants. Springer, Berlin. 404 pp.
- Little SA, RA Stockey, GW Rothwell 2006 *Stramineopteris aureopilosus* gen. et sp. nov.: reevaluating the role of vegetative anatomy in the resolution of leptosporangiate fern phylogeny. *Int J Plant Sci* 167:683–694.
- Mindell RA, RA Stockey, GW Rothwell, G Beard 2006 *Gleichenia appianensis* sp. nov. (Gleicheniaceae): a permineralized rhizome and associated vegetative remains from the Eocene of Vancouver Island, British Columbia. *Int J Plant Sci* 167:639–647.
- Novacek MJ, QD Wheeler 1992 Introduction. Pages 1–16 in MJ Novacek, QD Wheeler, eds. Extinction and phylogeny. Columbia University Press, New York.
- Pryer KM, E Schuettpelz, PG Wolf, H Schneider, AR Smith, C Raymond 2004 Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *Am J Bot* 91:1582–1598.
- Pryer KM, AR Smith, JE Skog 1995 Phylogenetic relationships of extant ferns based on evidence from morphology and *rbcL* sequences. *Am Fern J* 85:205–282.
- Rothwell GW 1987 Complex Paleozoic Filicales in the evolutionary radiation of ferns. *Am J Bot* 74:458–461.
- 1999 Fossils and ferns in the resolution of land plant phylogeny. *Bot Rev* 65:188–218.
- Rothwell GW, KC Nixon 2006 How does the inclusion of fossil data change our conclusions about the phylogenetic history of euphyllophytes? *Int J Plant Sci* 167:737–749.
- Rothwell GW, RA Stockey 2006 Combining characters of Pteridaceae and tree ferns: *Pterisorus radiata* gen. et sp. nov., a permineralized Lower Cretaceous filicalean with radial sori. *Int J Plant Sci* 167:695–701.
- Serbet R, GW Rothwell 2006 Anatomically preserved ferns from the Late Cretaceous of western North America. II. Blechnaceae/Dryopteridaceae. *Int J Plant Sci* 167:703–709.
- Smith AR 1995 Non-molecular phylogenetic hypotheses for ferns. *Am Fern J* 85:104–122.
- Smith SY, RA Stockey, H Nishida, GW Rothwell 2006 *Trawetsia princetonensis* gen. et sp. nov. (Blechnaceae): a permineralized fern from the Middle Eocene Princeton Chert. *Int J Plant Sci* 167:711–719.
- Stewart WN, GW Rothwell 1993 Paleobotany and the evolution of plants. Cambridge University Press, Cambridge. 521 pp.
- Stockey RA, TC Lantz, GW Rothwell 2006a *Speirseopteris orbiculata* gen. et sp. nov. (Thelypteridaceae), a derived fossil filicalean from the Paleocene of western North America. *Int J Plant Sci* 167:729–736.
- Stockey RA, GW Rothwell, SA Little 2006b Relationships among fossil and living Dipteridaceae: anatomically preserved *Hausmannia* from the Lower Cretaceous of Vancouver Island. *Int J Plant Sci* 167:649–663.
- Taylor TN, EL Taylor 1993 The biology and evolution of fossil plants. Prentice-Hall, Englewood Cliffs, NJ. 982 pp.
- Tidwell WD, SR Ash 1994 A review of selected Triassic to Early Cretaceous ferns. *J Plant Res* 107:417–442.
- Tomescu AMF, GW Rothwell, ML Trivett 2006 Kaplanopteridaceae fam. nov., additional diversity in the initial radiation of filicalean ferns. *Int J Plant Sci* 167:615–630.
- Trivett ML, RA Stockey, GW Rothwell, G Beard 2006 *Paralygodium vancouverensis* sp. nov. (Schizaeaceae): additional evidence for filicalean diversity in the Paleogene of North America. *Int J Plant Sci* 167:675–681.
- Vavrek MJ, RA Stockey, GW Rothwell 2006 *Osmunda vancouverensis* sp. nov. (Osmundaceae), permineralized fertile frond segments from the Lower Cretaceous of British Columbia, Canada. *Int J Plant Sci* 167:631–637.