

INTRODUCTION TO THE DARWIN SPECIAL ISSUE: THE ABOMINABLE MYSTERY¹

RUTH A. STOCKEY,^{2,5} SEAN W. GRAHAM,³ AND PETER R. CRANE⁴

²Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9 Canada; ³UBC Botanical Garden & Centre for Plant Research (Faculty of Land and Food Systems), 2357 Main Mall, and Department of Botany, 6270 University Boulevard, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada; and ⁴Department of the Geophysical Sciences, The University of Chicago, 5734 S. Ellis Avenue, Chicago, Illinois 60637 USA

This February marks the 200th anniversary of Charles Darwin's birth, and later in the year we will also celebrate the 150th anniversary of the publication of *On The Origin of Species*. Reflecting on how Darwin influenced the field of botany, and in honor of his bicentennial, we have brought together a series of 21 papers that explore just one of the many botanical issues that Darwin commented on, what has come to be known as his "abominable mystery": the origin, rapid diversification, and rise to dominance of the angiosperms (flowering plants). While Darwin wrote several books devoted exclusively to botanical topics, he said relatively little about large-scale patterns of plant evolution, but this famous phrase, from a letter he wrote to Sir Joseph Hooker in 1879, has been widely quoted. The phrase has become a symbol of a key gap in our understanding of plant evolution. A portion of the original letter in Darwin's hand appears on our back cover.

Over the years, the way in which generations of botanists have used this quotation has come to differ greatly from what Darwin originally intended. The first paper in this issue by Friedman (2009) explores what Darwin meant when he first used the phrase "abominable mystery." Friedman traces the factors that influenced Darwin's thinking at the time, based on his study of Darwin's correspondence with prominent botanists and paleobotanists of the day.

Our issue then turns to the evolution of one of the most distinctive and evolutionarily important features of angiosperms, the flower. Endress and Doyle (2009) discuss the "ancestral angiosperm flower" and consider its likely initial specializations by integrating ideas from anatomy, morphology, paleobotany, and phylogeny. Their paper sets the stage for others that consider additional aspects of early flower evolution from a variety of perspectives. These include the difficulties of distinguishing between flowers and inflorescences in some ancient lineages of angiosperms (Rudall et al., 2009), the molecular developmental genetics of petal evolution (Hileman and Irish, 2009; Rasmussen et al., 2009), and floral variation and floral genetics (P. Soltis et al., 2009). Papers using comparative data from living flowering plants to reconstruct the early evolution of the angiosperm megagametophyte (Friedman and Ryerson, 2009) and the progamic phase (Williams, 2009), add further comparative developmental perspectives to the evolution of one of the most distinctive attributes of angiosperms, the accelerated and truncated life cycle.

Charles Darwin was a pioneer in the study of angiosperm flowers and how they function. He contributed many original

insights, but he was intrigued by the ideas of Gaston de Saporta (1885) who suggested that insects and their role in pollination were of critical importance in the evolution and diversification of angiosperms (Friedman, 2009). Two papers in the issue deal with pollination biology (Thien et al., 2009) and postpollination function of the transmitting tissue in ancient lineages of angiosperms (Sage et al., 2009).

The phylogenetic framework developed for early angiosperm evolution over the last twenty years (Doyle and Endress, 2009) has been an important catalyst for many of the comparative and developmental studies included in the first part of the issue. It has also focused renewed attention on other features that have traditionally been central in discussions of angiosperm evolution, including vegetative structure. In their study of xylem in Nymphaeaceae, Carlquist et al. (2009) demonstrate that detailed analyses of these features can still bring to light important new insights.

The aspect of angiosperm evolution that remains the most mysterious is their relationship to other groups of living and fossil seed plants. This issue is taken up in relation to living groups of seed plants by Graham and Iles (2009) who explore alternative approaches to pinpointing the root of the flowering plant tree, key to making inferences about the direction of evolutionary transitions in early angiosperms. They ask whether inferences of the angiosperm root node are negatively influenced by the long branches separating angiosperms from gymnosperms in molecular phylogenies. Mathews (2009) also discusses current knowledge of the phylogenetic relationships of seed plants based on molecular approaches and highlights two key issues: what are the persistent phylogenetic questions, and what are the limits of molecular data in resolving them?

The paleobotanical record as it was understood by Darwin and his correspondents, such as Oswald Heer and Gaston de Saporta, in the late nineteenth century (Friedman, 2009) has changed dramatically. The practice of assigning poorly understood fossils to modern genera of angiosperms has been replaced by a more sophisticated understanding of the importance of mosaic evolution and more realistic assessments of the different lineages of angiosperms present during the Early Cretaceous. What looked like a very rapid evolution of modern taxa to Darwin and his colleagues, we now know was in part a false impression created by uncritical taxonomic assignments. Nevertheless, by any measure, the initial diversification and rise to dominance of angiosperms was still remarkably rapid. Darwin speculated that the seemingly sudden appearance of flowering plants reflected an origin in a remote place, perhaps the Southern Hemisphere, which resulted in a poorly known fossil record (Friedman, 2009). Among the paleobotanical papers in this volume is an assessment by Taylor and Taylor (2009) of what we know of the fossil record of gymnosperms from the Southern Hemisphere.

¹ Manuscript received 3 December 2008; revision accepted 8 December 2008.

⁵ Author for correspondence (e-mail: ruth.stockey@ualberta.ca)

Of the potential close relatives of angiosperms suggested by both molecular and morphological studies, certain groups of plants emerge repeatedly as perhaps having particular significance. These include extinct Caytoniales and Bennettitales, as well as extant Gnetales. Bennettitales (Cycadeoidales) are addressed in three separate articles in this issue. The first of these by Friis et al. (2009), including data from Portugal and eastern North America, discusses relationships among Bennettitales, Erdtmanithecales, and Gnetales and describes several new fossil taxa relevant to this issue. The second, by Crane and Herendeen (2009), presents new data on Bennettitales from the classic Middle Jurassic flora of Yorkshire, which has provided important information on the structure of this extinct group. The third, by Rothwell et al. (2009), discusses Bennettitales in the context of the anthophyte hypothesis (Doyle and Donoghue, 1987) and provides important new data on reproductive structures of the Bennettitales from specimens with well-preserved internal anatomy. This paper presents contrasting views on the biology and reproductive structures of the Bennettitales using the anatomy of seeds and cones.

Fossil gymnosperms are also addressed in the paper by Stockey and Rothwell (2009), which describes a new fruit-like reproductive structure from the Lower Cretaceous of Vancouver Island. This paper explores the evolution of the carpel and the second integument in flowering plants and touches on the problem of recognizing the earliest angiosperms when we find them in the fossil record.

The final three papers by Doug Soltis et al. (2009), Magallón and Castillo (2009), and Crepet and Niklas (2009) provide a large-scale overview of different facets of angiosperm diversification and “success.” Doug Soltis et al. (2009) assess the likely importance of polyploidy as a major force in angiosperm diversification, while Magallón and Castillo (2009) provide estimates of the diversification rate of angiosperms at the level of major clades (orders) through time. Finally, Crepet and Niklas (2009) probe possible reasons for flowering plant success that may have favored high speciation rates, low extinction rates or broad ecological tolerances.

Just as Darwin and his contemporaries did not agree on their scientific theories, our authors provide diverse expertise, different perspectives and sometimes contrasting opinions on many of the topics presented here. There is much about early angiosperm evolution that remains mysterious. Nevertheless, we hope that this special issue of the *American Journal of Botany* documents some important areas of progress, provides an up-to-date view of prevailing ideas on angiosperm origins, and contributes new perspectives that will be useful guides for future research.

LITERATURE CITED

- CARLQUIST, S., E. L. SCHNEIDER, AND C. B. HELLQUIST. 2009. Xylem of early angiosperms: *Nuphar* (Nymphaeaceae) has novel tracheid microstructure. *American Journal of Botany* 96: 207–215.
- CRANE, P. R., AND P. S. HERENDEEN. 2009. Bennettitales from the Grisetorpe Bed (Middle Jurassic) at Cayton Bay, Yorkshire, UK. *American Journal of Botany* 96: 284–295.
- CREPET, W. L., AND K. J. NIKLAS. 2009. Darwin’s second “abominable mystery”: Why are there so many angiosperm species? *American Journal of Botany* 96: 366–381.
- DE SAPORTA, L. C. J. G., AND A.-F. MARION. 1885. L’évolution du règne végétal. Les Phanérogames. Ancienne Librairie Germer Baillière, Saint-Germain, France.
- DOYLE, J. A., AND M. J. DONOGHUE. 1987. The origin of angiosperms: A cladistic approach. In E. M. Friis, W. G. Chaloner, and P. R. Crane [eds.], *The origins of angiosperms and their biological consequences*. Cambridge University Press, Cambridge, UK.
- ENDRESS, P. K., AND J. A. DOYLE. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *American Journal of Botany* 96: 22–66.
- FRIEDMAN, W. E. 2009. The meaning of Darwin’s “abominable mystery.” *American Journal of Botany* 96: 5–21.
- 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.
- FRIIS, E. M., K. R. PEDERSEN, AND P. R. CRANE. 2009. Early Cretaceous mesofossils from Portugal and eastern North America related to the Bennettitales-Erdtmanithecales-Gnetales group. *American Journal of Botany* 96: 252–283.
- GRAHAM, S. W., AND W. J. D. ILES. 2009. Different gymnosperm outgroups have (mostly) congruent signal regarding the root of flowering plant phylogeny. *American Journal of Botany* 96: 216–227.
- HILEMAN, L. C., AND V. F. IRISH. 2009. More is better: The uses of developmental genetic data to reconstruct perianth evolution. *American Journal of Botany* 96: 83–95.
- MAGALLÓN, S., AND A. CASTILLO. 2009. Angiosperm diversification through time. *American Journal of Botany* 96: 349–365.
- MATHEWS, S. 2009. Phylogenetic relationships among seed plants: Persistent questions. *American Journal of Botany* 96: 228–236.
- RASMUSSEN, D. A., E. M. KRAMER, AND E. A. ZIMMER. 2009. One size fits all? Molecular evidence for a commonly inherited petal identity program in the Ranunculales. *American Journal of Botany* 96: 96–109.
- ROTHWELL, G. W., W. L. CREPET, AND R. A. STOCKEY. 2009. Is the anthophyte hypothesis alive and well? New evidence from the reproductive structures of Bennettitales. *American Journal of Botany* 96: 296–322.
- RUDALL, P. J., M. V. REMIZOWA, G. PRENNER, C. J. PRYCHID, R. E. TUCKETT, AND D. D. SOKOLOFF. 2009. Nonflowers near the base of extant angiosperms? Spatiotemporal arrangement of organs in reproductive units of Hydatellaceae and its bearing on the origin of the flower. *American Journal of Botany* 96: 67–82.
- SAGE, T. L., K. HRISTOVA-SARKOVSKI, V. KOEHL, J. LYEW, V. PONTIERI, P. BERNHARDT, P. WESTON, et al. 2009. Transmitting tissue architecture in basal-relictual angiosperms: Implications for transmitting tissue origins. *American Journal of Botany* 96: 183–206.
- SOLTIS, D. E., V. A. ALBERT, J. LEEBENS-MACK, C. D. BELL, A. H. PATERSON, C. ZHENG, D. SANKOFF, et al. 2009. Polyploidy and angiosperm diversification. *American Journal of Botany* 96: 336–348.
- SOLTIS, P. S., S. F. BROCKINGTON, M.-J. YOO, A. PIEDRAHITA, M. LATVIS, M. J. MOORE, A. S. CHANDERBALI, AND D. E. SOLTIS. 2009. Floral variation and floral genetics in basal angiosperms. *American Journal of Botany* 96: 110–128.
- STOCKEY, R. A., AND G. W. ROTHWELL. 2009. Distinguishing angiosperms from the earliest angiosperms: A Lower Cretaceous (Valanginian-Hauterivian) fruit-like reproductive structure. *American Journal of Botany* 96: 323–335.
- TAYLOR, E. L., AND T. N. TAYLOR. 2009. Seed ferns from the late Paleozoic and Mesozoic: Any angiosperm ancestors lurking there? *American Journal of Botany* 96: 237–251.
- THIEN, L. B., P. BERNHARDT, M. S. DEVAL, Z.-D. CHEN, Y.-B. LUO, J.-H. FAN, L.-C. YUAN, AND J. H. WILLIAMS. 2009. Pollination biology of basal angiosperms (ANITA grade). *American Journal of Botany* 96: 166–182.
- WILLIAMS, J. H. 2009. *Amborella trichopoda* (Amborellaceae) and the evolutionary developmental origins of the angiosperm progamic phase. *American Journal of Botany* 96: 144–165.