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# CELEBRATING GIANT STEPS TOWARD A SYNTHETIC HISTORY OF ANGIOSPERM EVOLUTION

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The emergence of *Amborella trichopoda* as the sister to all other extant angiosperms (Mathews and Donoghue 1999; Qiu et al. 1999) marked the beginning of an important decade for plant phylogenetics. Since that time, enormous progress has been made toward understanding the fundamental structure of angiosperm phylogeny (Cantino et al. 2007; Moore et al. 2007; APG 2009). For instance, we are now confident in the basal grade of angiosperms, in the existence of eudicots, and in the relationships among the major monocot and eudicot lineages. This resolution provided immediate clarity on some old outstanding hypotheses about early angiosperm evolution: the first angiosperms did not have large magnolia-type flowers (Endress and Doyle 2009; Doyle and Endress 2010), and they likely lived in wet, shady environments (Feild et al. 2004). Many of the inferences derived from extant angiosperms have been confirmed with new evidence from the fossil record (Friis et al. 2011).

But these basic phylogenetic advances have provided new insight on many other problems in flowering plant evolution. Perhaps the most obvious have been the advances in understanding the genetic underpinnings of floral organ identity (Irish 2003; Chanderbali et al. 2010) and, to a lesser degree, floral symmetry (Preston and Hileman 2009). New genome-scale information has confirmed the importance of polyploidy in flowering plant evolution, with inferred whole-genome duplication events, both ancient and recent, scattered throughout seed plant evolution (Jiao et al. 2011; Leitch and Leitch 2012). Our increasing ability to build ever-larger phylogenies is allowing a new bird's-eye view on some specific problems (e.g., Smith and Donoghue 2008), and better taxon sampling and improved methods for dating phylogenies are providing first looks at the tempo and mode of diversification within flowering plants (e.g., Richardson et al. 2001; Hughes and Eastwood 2006; Bytebier et al. 2010; Marazzi and Sanderson 2010; Arakaki et al. 2011) and, occasionally, the potential influence of angiosperms on the diversification of other groups (Schneider et al. 2004; Moreau et al. 2006).

At the same time, a phylogenetic perspective has been seeping into an increasingly diverse array of research questions. These nascent interfaces have already added bold new dimensions to our understanding of the angiosperm rise to dominance. Evolution clearly influences the "ecological theater" (sensu Hutchinson 1965) in which it operates, and angiosperms in particular have played strong roles in changing the global environment (Pagani et al. 2009; Boyce and Lee 2010; Feild et al. 2011). We are in the midst of a second wave in the phylogenetic revolution, in terms of who pays attention to phylogenies and how they are used to interpret novel types of data. This special issue is a celebration of this new integration—an insurgence of phylogenetic thinking into fields as far flung as atmospheric $CO_2$ modeling and fire ecology. We provide several nods to familiar angiosperm-centric themes, such as reproduction, vessel evolution, growth form, shade tolerance, and alternative photosynthetic pathways, though our aim is to provide a more holistic perspective on these issues by encouraging each contributor to address his or her particular topic with evidence from multiple disciplines (e.g., paleobotany, paleoclimatology, plant physiology, and/or development). We highlight angiosperm influence on other lineages that are their important counterparts, such as conifers, ferns, and fungi. We also emphasize the role of angiosperms in shaping modern ecosystem structure and function via their interaction with fire, water, and biogeochemical cycles; their total domination of the herbaceous growth form; and their creation of previously nonexistent environments such as deep shade.

Some subjects are decisively missing from this issue, and we would like to highlight them as wide-open areas of research. For example, we understand very little about fruit evolution; though flowers and fruits are both novel structures resulting from the origin of the carpel, floral evolution and function have clearly received the lion's share of attention. In terms of ecosystem-angiosperm interactions, the clustering of many origins of nitrogen-fixing plants in one region of the rosid clade remains stubbornly mysterious (but see Markmann et al. 2008). While it has been suggested that there has been strong filtering of angiosperm lineages during colonization of the colder environments that formed during the Miocene to Pleistocene (Donoghue 2008), this has never been examined in any real way, and we know very little about the evolution of cold adaptation. This is just a very short laundry list of low-hanging fruit; the next decade will see enormous advances in each of these topics, plus many more.

In general, increased phylogenetic resolution usually brings increased subtlety to our understanding of evolutionary adaptation and success. Key innovations become key opportunities (de Queiroz 2002); discrete character states dissolve into many varied and overlapping forms (Carlquist and Schneider 2002; Christin et al. 2011); oddball taxa that were once simple curiosities become highly informative (Edwards and Donoghue 2006; Saarela et al. 2007). If you asked a botanist 20 years

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ago, "What was the real innovation of angiosperms—why did they take over the world?" inevitably he or she would have suggested the flower, because the flower is the synapomorphy of angiosperms. Today, you are likely to get a variety of less assured answers. Some will still suggest flowers, others high venation density. Some might discuss mycorrhizal symbioses. Others will argue for polyploidy and still others the alteration and subsequent tolerance of low atmospheric $CO_2$. We say: all of the above. Clearly! Angiosperms are multifaceted in their remarkable uniqueness. Eventually, the relative importance of these (and other) innovations will be sorted, in space and in time. But for now, enjoy this moment of discovery and excitement—help us celebrate the enormous and wonderful wilderness of the flowering plant revolution.

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