Ancient WGD Events as Drivers of Key Innovations in Angiosperms

Pamela S. Soltis^{1,2} and Douglas E. Soltis^{1,2,3}

¹Florida Museum of Natural History

²Genetics Institute

³Department of Biology

University of Florida

Gainesville, FL, USA

Polyploidy, or whole-genome duplication (WGD), is a ubiquitous feature of plant genomes, contributing to variation in both genome size and gene content. Although polyploidy has occurred in all major clades of land plants, it is most frequent in angiosperms. Following a WGD in the common ancestor of all extant angiosperms, a complex pattern of both ancient and recent polyploidy is evident across angiosperm phylogeny. In several cases, ancient WGDs are associated with increased rates of species diversification. For example, a WGD in the common ancestor of Asteraceae, the largest family of angiosperms with ~25,000 species, is statistically linked to a shift in species diversification; several other old WGDs are followed by increased diversification after a 'lag' of up to three nodes. WGD may thus lead to a genomic combination that generates evolutionary novelty and may serve as a catalyst for diversification. In this paper, we explore possible links between WGD, the origin of novelty, and key innovations and propose a research path forward.

Polyploidy and Novelty

Polyploidy has long been recognized as a source of genetic, biochemical, and evolutionary novelty (e.g., Roose and Gottlieb 1976; Levin 1983; Soltis et al. 2014, 2015). Duplicate gene pairs in allopolyploids result in novel enzyme phenotypes, which may in turn have downstream phenotypic effects, relative to the diploid progenitors (Roose and Gottlieb 1976). Beyond the novel phenotypes conferred by gene duplication, nucleotypic effects due merely to the increased size of the nucleus may be manifested as novelty in physiological, phenological, anatomical, morphological, and other traits in both auto- and allopolyploids (Levin 1983). Extensive variation in gene content, gene expression, and

karyotype within and among populations of naturally occurring and recently formed (within the past 80 years) allopolyploids in *Tragopogon* (Asteraceae) (e.g., Buggs et al. 2011, 2012; Chester et al. 2012; Soltis et al. 2012) produces mosaics of genetically and phenotypically variable traits in novel combinations (e.g., Soltis et al. 2014, 2015). This novelty that arises on a microevolutionary scale may ultimately lead to a unique trait that drives evolutionary diversification at the macroevolutionary level (Soltis et al. 2015).

Key Innovations

Key innovations are generally defined as novel phenotypic traits that result in evolutionary radiations (although Miller (1949) initially referred to them as adjustments that led to the origin of new major groups of organisms). Although the concept of key innovations has been criticized on grounds ranging from difficulty in associating specific traits with increased diversification to problems of inferring causality even when such an association is demonstrated (e.g., Cracraft 1990; Galis 2001). A host of comparative methods enables statistical analysis of trait-specific diversification (e.g., the BiSSE family of methods, Maddison et al. 2007; BAMM, Rabosky 2014; but see Moore et al. submitted), and application of these approaches in conjunction with improved phylogenetic hypotheses certainly improves the ability to link specific features to increased diversification.

However, perhaps a more compelling criticism of the concept of key innovations concerns the fact that an observed trait may actually be decomposed into a series of evolutionary changes that eventually culminate in a “trait” (or traits) that lead to increased diversification (Donoghue 2005); thus, identifying the single step that constitutes the “key” in a series may be difficult, if not impossible, particularly as the multi-step innovation may

itself be spread across multiple nodes. These criticisms notwithstanding, the concept of key innovations remains a useful model for exploring the link between character evolution and species diversification. In angiosperms, several features have been identified as key innovations: the bipartite perianth of sepals and petals in eudicots, syncarpy with a compitum (a tract of [transmission tissue](#) in the gynoecium that is common to all the carpels of one flower and that allows pollen landing on a stigma or part of a stigma to fertilize ovules in any carpel, Missouri Botanical Garden,

http://www.mobot.org/mobot/research/apweb/top/glossarya_h.html#C)

in most core eudicots and most monocots, tenuinucellate ovules in asterids, sympetaly in asterids, and fusion of stamens with petals in euasterids (Endress 2006). Moreover, many structural innovations in the flower mark specific clades and are also hypothesized as key innovations (Endress 2011).

The flower itself can be seen as a key innovation, yet the flower as a ‘trait’ certainly exemplifies the case of an innovation as a series of steps, in this case, the origin of perianth, stamens, and carpels, plus the more complex feature of double fertilization. Despite conceptual advances in the nature of key innovations themselves, the genetic origins of key innovations are largely unknown. What genes control the expression of a key innovation, and how were these genes assembled? With respect to the flower, an ancient WGD in the common ancestor of angiosperms was hypothesized to have produced an array of duplicate genes that in turn ultimately led to the origin of the flower (e.g., Buzgo et al., 2005; De Bodt et al. 2005; Zahn et al. 2005), all prior to the evidence for this ancient WGD (Jiao et al. 2011). Specifically, duplications in MADS-box genes provided the genetic material for the origin of transcription factors that control the specification of floral organs. Most notably,

gene duplication led to the *APETALA3/PISTILLATA* gene lineages that control B function in floral development, i.e., the specification of petals and stamens, when expressed in concert with A-function and C-function genes, respectively (Fig. 1; Coen and Meyerowitz 1991; see Kim et al. 2004 for *AP3/PI* gene phylogeny). Likewise, the *AGAMOUS* gene lineage, which confers C function (specifying stamen identity when expressed with B-function genes and carpel identity when expressed alone), is sister D-function lineage (Kramer et al. 2004), which specifies ovule development in angiosperms. Also required for floral organ specification is expression of a set of *SEPALLATA* genes, which also trace their duplication history to the common ancestor of the angiosperms (Zahn et al. 2005). These specific cases exemplify a pattern exhibited by many other genes – at least 10% of all floral regulators in *Arabidopsis thaliana* trace back to the common ancestor of all angiosperms – based on analysis of the genome of *Amborella trichopoda*, sister to all other extant angiosperms (*Amborella* Genome Project 2013). Thus, the WGD that preceded the origin of the angiosperms clearly contributed genetic fodder that appears to have resulted in the key innovation we know as the flower. Is it possible that other WGDs are likewise associated with key innovations in the angiosperms?

WGDs and Key Innovations

Recent evidence indicates that many WGDs in angiosperms are associated with increased rates of diversification (Tank et al. 2015). Moreover, many deep WGD events in angiosperms seem to be associated with one or more key innovations (Fig. 2). We briefly review select examples here, emphasizing the early evolution of angiosperms and the subsequent origins of major clades. For each example, we describe the WGD, the node of

angiosperm phylogeny with which it is associated, subsequent radiation, and putative key innovation itself. Our final example, the evolution of glucosinolate compounds in Brassicales (Edger et al. 2015), is a model for how such linkages among WGDs, duplicate genes, key innovations, and diversification can reveal significant patterns and processes of evolution.

The WGD that immediately preceded or coincided with the evolution of the angiosperms (Jiao et al. 2011, described above in the context of the origin of the flower itself) was subsequently followed after a lag by the “Big Bang” of angiosperm evolution (Moore et al. 2007)—the rapid radiation of the *Mesangiospermae* (all remaining angiosperms after the ANA grade of *Amborella*, Nymphaeales, and Austrobaileyales, per Soltis et al. 1999, 2000; Angiosperm Phylogeny Group 2016). Associated with that node is the evolution of several key angiosperm features, most notably the developmentally sealed carpel (rather than sealed by mucilage) and true vessel elements in stem tissue. The carpels of *Amborella*, the sister to all other living angiosperms, as well as *Cabomba* and *Brasenia* of Nymphaeales and *Austrobaileya*, *Trimenia*, and *Kadsura* of Austrobaileyales, are closed by secretion rather than congenital fusion (Endress and Igersheim 2000). Although some degree of actual fusion occurs in *Nymphaea* (Nymphaeales) and *Illicium* (Austrobaileyales), the congenitally fused carpel is most likely a synapomorphy for *Mesangiospermae* (although carpels of *Ascarina* (Chloranthales) are also closed by secretion) (Endress and Igersheim 2000; Endress 2005; see review by Soltis et al. 2009 for discussion of the possible genetic control of this feature). Likewise, *Amborella* lacks vessel elements in stem tissue, as do the aquatic Nymphaeales (although vessel elements are present in roots). Austrobaileyales have water-conducting cells considered intermediate

between tracheids and true vessels (Carlquist and Schneider 2001, 2002); thus, true vessels seem to have originated following the divergence of Austrobaileyales from the rest of the angiosperms, likely also in the common ancestor of the *Mesangiospermae*.

More recently within the angiosperms are possible key innovations associated with the diversification of *Pentapetalae* (all core eudicots other than Gunnerales; representing approximately 70% of all angiosperm species), the monocots, and Compositae. The γ hexaploidy event (probably two WGD events in close succession) occurred somewhere during the evolution of basal eudicots (Jiao et al. 2012) and was followed closely by the origin and rapid radiation of *Pentapetalae*. Associated with the origin of *Pentapetalae* is the five-merous floral groundplan, as well as chemical characters (e.g., gallic acid; see Soltis et al. 2005, 2016).

The shift to a pentamerous groundplan in *Pentapetalae* involved at least three steps (see Chanderbali, Berger, et al. 2016): (1) two WGDs (γ , described above) shortly before the diversification of *Pentapetalae*, (2) maintenance of duplicate gene copies (perhaps resulting from these WGDs) that interact and control organ identity, symmetry, fusion, polarity, elongation, and growth and could thus have contributed functions that led to the origin of the whorled, pentamerous flower, and (3) a shift from the “fading borders” model of floral gene expression typical of basal angiosperms and basal eudicots to the canonical ABCE model (Fig. 1) in *Pentapetalae*. Despite independent observations of these three crucial steps, the connections between them require further study: Where, in fact, during eudicot phylogeny did the two WGDs occur? Do the duplicate floral regulators actually trace to ancient WGDs? How do these duplicate genes interact, and do their interactions lead to the observed shifts in floral morphology (i.e., pentamery, whorled floral organ

arrangements, differentiated perianth into sepals and petals)? Where phylogenetically did the shift from the fading borders to the ABCE model occur? Answers to these questions will lead to greater understanding of the genetic basis for the origin of the ABCE floral groundplan and will help resolve one of the major mysteries of angiosperm evolution.

The origin of the monocots, with ~65,000 species, is also associated with a WGD event, τ (Paterson et al. 2012). Recent sequencing of additional monocot genomes, such as pineapple (Ming et al. 2015) and additional grasses (Estep et al. 2014), has confirmed this WGD. However, repeated rounds of WGDs within monocots have yielded complex patterns of both retained duplicate genes and macroevolutionary diversification. Despite numerous WGDs within monocots, the placements of these ancient events remain uncertain because of limited sampling. Additional data (genomes, transcriptomes) from a more comprehensive sampling of species are needed to place these WGDs. Until then, it will be difficult to tease apart those gene duplications that trace to the monocot-wide WGD, τ , from those derived from more recent WGDs.

Numerous morphological features accompanied the origin of the monocots including: single cotyledon, scattered vascular bundles, calcium oxalate raphides, successive microsporogenesis, and adventitious roots. However, despite evidence for WGD and an array of unique features that characterize the monocots, at this point linking specific duplicate genes to morphological and anatomical innovations is intractable. Moreover, although monocots clearly evolved under an increased rate of species diversification (Tank et al. 2015), whether that shift occurred immediately after WGD or following a lag is not clear. In contrast, grasses, which are marked by a WGD of their own, do not appear to have undergone an increased rate of diversification, although allopolyploidy is an important

mode of speciation (Estep et al. 2014). Finally, the origin of so many unique features in the common ancestor of monocots may have led to this radiation and the subsequent diversification of monocots into unique habitats and ecological space, but the plurality of traits precludes identification of a single key innovation. Instead, the 'key innovation' may be the suite of accumulated traits (per Donoghue's (2005) model); in fact, these traits may have arisen in a stepwise manner, but these plants are now extinct, and the signature of these cumulative innovations is gone. Thus, our view of WGD leading to morphological/anatomical/chemical novelty and then radiation is not clearly testable in monocots, despite the three key ingredients of WGD, novel traits, and increased rates of diversification.

A WGD event is associated with the origin of Compositae (or perhaps Compositae and its sister group, Calyceraceae; Barker et al. 2008), a family characterized by the evolution of a distinctive inflorescence, pollen presentation mechanism, and chemistry (sesquiterpene lactones) (Judd et al. 2015; Soltis et al. 2015). Compositae are the largest angiosperm family, with ~25,000 species (Judd et al. 2015). Although families are human constructs and cannot be compared biologically, Compositae are regardless a large clade marked by a WGD and multiple unique features. Furthermore, they exhibit an increased rate of diversification (Tank et al. 2015), and they are the sole clade in that study that has a perfect match of WGD and upward diversification rate shift. The inflorescence structure and pollen presentation mechanism could both confer enhance reproductive capacity, thus leading to the observed radiation, although plunger pollination in a different form is also a possible synapomorphy for Asterales as a whole (Judd et al. 2015). The chemical novelty and complexity of Compositae may also have played a role in diversification of the clade,

through enhanced protection from herbivory. However, the genetic control of these features is far from understood, despite outstanding studies of floral genetics in *Gerbera* (Teeri et al. 2006a, 2006b), and linking any of these features to duplicate genes derived from WGD remains elusive. Moreover, as with monocots, the co-phylogenetic occurrence of multiple traits in the common ancestor of crown Compositae makes identification of a key innovation in the classic sense particularly difficult.

Two WGD events occurred within Brassicales (referred to as α and β). The β event occurred soon after the origin of the clade (Fig. 3), and α coincided with the origin of Brassicaceae. A key innovation associated with Brassicales is the origin of glucosinolates and subsequent structural modifications. Brassicales represent the one clear example of how WGD events have resulted in key innovations in glucosinolate chemistry (Edger et al. 2015)—this chemical evolution in turn appears to be associated closely with bursts in speciation (Edger et al. 2015; Tank et al. 2015). We summarize this exciting linkage of WGD and key innovation below.

Glucosinolates arose in the ancestor of the Brassicales (Rodman et al. 2008). The first few branches of the clade are generally species poor (e.g., Akaniaceae, Caricaceae, Moringaceae). The β WGD event occurred in the ancestor of Limnanthaceae and remaining Brassicales—this event resulted in a duplication of genes in the glucosinolate pathway and the origin of indolic glucosinolates (Edger et al. 2015). This chemical innovation spurred subsequent diversification—the analyses of Tank et al. (2015) show a lag, but a closer match of WGD followed by diversification than in Edger et al. (2015). Similarly, the α WGD event resulted in a subsequent structural elaboration of glucosinolates, which then coincided (again with a lag) in a burst of diversification within Brassicaceae.

Testing Hypotheses of WGD and Key Innovations

In this paper, we have raised the hypothesis that WGDs provide a mechanism for the origin of evolutionary novelty, specifically in the form of key innovations that may have triggered radiations during angiosperm evolution. While the case for certain key innovations – such as the flower itself and key glucosinolate compounds – is supported by specific genetic links, the genetic underpinnings of most key innovations are unknown. We have taken an admittedly speculative approach, with the goal of stimulating new research into the connection among WGDs, radiation, key innovations, and their underlying genes, and suggest the following avenues for future research (see also Wagner and Lynch 2010). Testing of these connections requires: (i) clear phylogenetic placement of putative key innovations; (ii) clear phylogenetic placement of WGDs; (iii) tests of diversification rate shifts associated with putative key innovations and with WGDs; (iv) tests of trait-specific diversification – are putative key innovations statistically associated with both WGDs and rate shifts?; and (v) ties of putative key innovations to underlying genetics/duplicate genes/WGDs. Given the repeated pattern of WGDs in the angiosperms and the observed lag between WGD and diversification, analyses of the role of duplicate genes in the origin of key innovations must consider duplicate genes that trace to the most recent WGD and not an earlier one. This relationship of key innovation to recent WGD is evident for floral genes duplicated prior to the origin of angiosperms and for chemistry in Brassicales, but is lacking for the other putative key innovations described in this paper. The analyses of radiations, WGDs, and chemical innovations by Edger et al. (2015) clearly provide a

paradigm for the manner of studies needed to explore the role of WGDs in generating novelty and spurring diversification in angiosperms.

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Figure Legends

Figure 1. The ABC model of floral organ identity showing combinatorial gene action specifying sepals, petals, stamens, and carpels, following Coen and Meyerowitz (1991). Modified from Chanderbali, Berger, et al. (in press). In *Arabidopsis*, the A-function (conferred by *APETALA1*) specifies sepals, A- and B-function (*APETALA3* AND *PISTILLATA*) specify petals, B- and C-function (*AGAMOUS*) specify stamens, and C-function alone specifies carpels. E-function, which is conferred by a set of duplicate *SEPALLATA* genes, is required in conjunction with other floral regulators for correct organ specification. The organs that compose a flower are derived from sterile leaves, perhaps through the action of duplicate genes that arose in the common ancestor of the angiosperms, most likely through WGD. Duplicate gene copies (*APETALA3/PISTILLATA*) specify the developmental identity of petals and stamens in particular, with duplicate *SEPALLATA* genes modulating their expression. Given that many elements of the floral organ identity model are conserved across all angiosperms, including the most ancient lineages (see Chanderbali, Berger, et al., 2016), the WGD that preceded the origin of the angiosperms may have provided the genetic fodder that was eventually shaped into the floral developmental pathway.

Figure 2. Diversification of angiosperms, showing phylogenetic placements of select WGDs and synapomorphies/key innovations. Green stars represent WGD events, circles represent rate shifts, with color indicating magnitude of increased diversification rate (see figure for scale). A. *Mesangiospermae*, showing fused carpels and vessel elements. B. Monocots, showing scattered vascular bundles and adventitious roots. C. *Pentapetalae*,

showing pentamorous flower and gallic acid. Phylogenetic tree modified from Tank et al. (2015). Images used by permission.

Figure 3. WGDs, key innovations, and diversification in Brassicales. From Edger et al. (2015). Used by permission.

Figure 1

Figure 2

Figure 3

Brassicales
Host-plants