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Phylogeny, divergence times, and historical biogeography of the angiosperm family Saxifragaceae

Jia-bin Deng [a,b,c], Bryan T. Drew [b,c,d,*], Evgeny V. Mavrodiev [c], Matthew A. Gitzendanner [b,c], Pamela S. Soltis [c], Douglas E. Soltis [b,c]

[a] *College of Life Science, Sichuan Agricultural University, Yaan, Sichuan 625014, China*
[b] *Department of Biology, University of Florida, Gainesville, FL 32611, USA*
[c] *Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA*
[d] *Department of Biology, University of Nebraska-Kearney, Kearney, NE 68849, USA*

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ABSTRACT

Saxifragaceae (Saxifragales) contain approximately 640 species and 33 genera, about half of which are monotypic. Due to factors such as morphological stasis, convergent morphological evolution, and disjunct distributions, relationships within Saxifragaceae have historically been troublesome. The family occurs primarily in mountainous regions of the Northern Hemisphere, with the highest generic and species diversity in western North America, but disjunct taxa are known from southern South America. Here, we integrate broad gene (56 loci) and taxon (223 species) sampling strategies, both the most comprehensive to date within Saxifragaceae, with fossil calibrations and geographical distribution data to address relationships, divergence times, and historical biogeography among major lineages of Saxifragaceae. Two previously recognized main clades, the heucheroids (eight groups + *Saniculiphyllum*) and saxifragoids (*Saxifraga* s.s.), were re-affirmed by our phylogenetic analyses. Relationships among the eight heucheroid groups, as well as the phylogenetic position of *Saniculiphyllum* within the heucheroids, were resolved with mostly high support. Divergence time estimates indicate that Saxifragaceae began to diversify ca. 38.37 million years ago (Mya; 95% HPD = 30.99–46.11 Mya) in the Mid-Late Eocene, and that the two major lineages, the heucheroids and saxifragoids, began to diversify approximately 30.04 Mya (95% HPD = 23.87–37.15 Mya) and 30.85 Mya (95% HPD = 23.47–39.33 Mya), respectively. We reconstructed ancestral geographic areas using statistical dispersal-vicariance (S-DIVA). These analyses indicate several radiations within Saxifragaceae: one in eastern Asia and multiple radiations in western North America. Our results also demonstrate that large amounts of sequence data coupled with broad taxon sampling can help resolve clade relationships that have thus far seemed intractable.

1. Introduction

Saxifragaceae, in the eudicot order Saxifragales (APG, 2009), contain approximately 640 species in 33 genera, about half of which are monotypic (Supplementary Table S1, Soltis, 2007; Soltis et al., 2001a). Saxifragaceae comprise two major lineages, the saxifragoids, which consist of *Saxifraga sensu stricto* (s.s. including *Saxifragella bicuspidata*, but excluding the genus *Micranthes*), and the heucheroids, which are subdivided into eight "groups" or subclades and contain all remaining genera (Supplementary Table S1, Soltis, 2007; Soltis et al., 2001a). Saxifragaceae are distributed primarily in the Northern Hemisphere, particularly in montane regions, with centers of diversity in western North America, East Asia, and the Himalayas. The greatest concentration of genera occurs in the Pacific Northwest region of North America. Notably, some species of *Saxifraga* (e.g., *S. muscoides*, *S. paniculata*), *Mitella* (*M. nuda*), and *Chrysosplenium* (*C. alternifolium* and *C. tetrandrum*) are circumboreal (Soltis, 2007; Spongberg, 1972; Winkler et al., 2012), and several genera (*Saxifraga*, *Chrysosplenium*, *Mitella*, *Tiarella*, *Astilbe*) possess disjunct distributions in the Northern Hemisphere between eastern Asia and western North America, or less often eastern Asia and eastern North America (Soltis, 2007; Xiang et al., 1998). In addition, several Saxifragaceae taxa have narrow distributions in southern South America, well separated from other Saxifragaceae. For example, the monotypic *Hieronymusia* is

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[*] Corresponding author at: Department of Biology, University of Nebraska-Kearney, Kearney, NE 68849, USA.

E-mail addresses: jiabindeng@126.com (J.-b. Deng), bdrewfb@yahoo.com (B.T. Drew), evgeny@ufl.edu (E.V. Mavrodiev), magitz@botany.ufl.edu (M.A. Gitzendanner), psoltis@flmnh.ufl.edu (P.S. Soltis), dsoltis@ufl.edu (D.E. Soltis).

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known only from a small area of Argentina and Bolivia (Gornall and Bohm, 1985), and the monotypic *Saxifragella* and *Saxifragodes* are poorly understood taxa endemic to the southern tip of South America in Tierra del Fuego. In addition, two species of *Chrysosplenium* (*C. valdivicum*, *C. macranthum*) occur in Tierra del Fuego (Hara, 1957), and several species of *Saxifraga* are also found in the Andes (Webb and Gornall, 1989).

Due to a combination of morphological stasis, convergent morphological evolution, and disjunct distributions, relationships within Saxifragaceae have historically confounded botanists. The traditional Englerian view of Saxifragaceae (Engler, 1930) encompassed genera now placed in diverse families across the rosid and asterid clades currently recognized. For example, Hydrangeaceae (asterid), *Parnassia* (Celestraceae; rosid), and Vahliaceae (asterid), among others, were all formerly assigned to Saxifragaceae (Engler, 1930; Morgan and Soltis, 1993). This paper adopts the more narrow circumscription defined by Morgan and Soltis (1993), Soltis et al. (1993), Soltis (2007), and followed by APG (2009). Even as narrowly defined, generic relationships within Saxifragaceae are problematic. This uncertainty is perhaps best exemplified by the fact that 18 of the 33 genera of Saxifragaceae are monotypic (see Supplementary Table S1). Taxa within the family are often similar in overall vegetative morphology but genera are differentiated by distinctive suites of floral and fruit characters. The complex taxonomic history of the family is reviewed by Morgan and Soltis (1993) and Soltis (2007).

During the past several decades a number of molecular phylogenetic studies have helped clarify relationships within the family (DeChaine et al., 2013; Johnson and Soltis, 1995; Johnson et al., 1994; Kuzoff et al., 1999; Morgan and Soltis, 1993; Prieto et al., 2013; Soltis and Soltis, 1997; Soltis et al., 1993; Soltis et al., 2001a; Soltis et al., 2001b; Soltis et al., 1996; Vargas, 2000; Xiang et al., 2012; Zhu et al., 2013). Despite this recent progress, however, the relationships among most large lineages (groups) of Saxifragaceae, particularly within the heucheroids, remain unclear.

Taxa within Saxifragaceae have been used as model groups for studying polyploid speciation (e.g., Brochmann et al., 1998; Godsoe et al., 2013; Ness et al., 1989; Segraves and Thompson, 1999; Segraves et al., 1999; Soltis and Doyle, 1987; Soltis and Rieseberg, 1986; Soltis and Soltis, 1989; Soltis and Soltis, 1999; Soltis and Soltis, 1988; Soltis and Soltis, 1989; Soltis et al., 1993; Soltis et al., 1992; Soltis et al., 1991; Soltis et al., 1990; Soltis et al., 1989a; Soltis et al., 1989b; Soltis, 1984; Wolf et al., 1990), biogeography/phylogeography (Oliver et al., 2006; Reisch, 2008; Szövényi et al., 2009; Westergaard et al., 2010), and evolution and diversification (Holten et al., 2006; Kuzoff et al., 2001; Kuzoff et al., 1999; Okuyama et al., 2005; Soltis et al., 2001a; Steen et al., 2000; Vargas et al., 1999; Winkler et al., 2012). The biogeography of Saxifragaceae is especially intriguing, and several studies have speculated as to how Saxifragaceae may have achieved their present distribution. For example, Soltis et al. (2001b) hypothesized that *Chrysosplenium* originated in eastern Asia with several independent migration events from Asia to the New World, and further proposed that the disjunct South American taxa may have been the result of an ancient long-distance dispersal event. More recently, Zhu et al. (2013) proposed that *Astilbe* originated in Asia, with at least three subsequent dispersals into North America, Japan, and tropical Asian islands, respectively. However, these hypotheses were not formally tested using dated phylogenies or biogeographic analyses.

Most previous phylogenetic studies within Saxifragaceae have focused on broad scale relationships within the family and have achieved relatively stable lineage circumscriptions (see Soltis, 2007). However, our understanding of relationships among major Saxifragaceae lineages, as well as a general understanding of the biogeographic history of the family and timing of diversification events, have been hampered by limited gene and taxon sampling. Increasing amounts of sequence data and wider taxon sampling have yielded better resolution, support, and evolutionary insights throughout the tree of life (Heath et al., 2008; Moore et al., 2007; Parfrey et al., 2010; Soltis et al., 2011), and have provided order to clades that had previously seemed intractable (e.g., Wurdack and Davis, 2009; Xi et al., 2012).

Prior phylogenetic studies of Saxifragaceae were unable to elucidate relationships among many of the heucheroid lineages, and the placement of the monotypic *Saniculiphyllum* remains unclear. Here we present the most comprehensive Saxifragaceae phylogeny to date. We employed 56 plastid (cpDNA) and nuclear ribosomal DNA gene regions, sampled over 223 taxa, and included representatives from 32 of the 33 Saxifragaceae genera in an effort to clarify relationships among major lineages and explore when and where these lineages diversified. Specifically, we address the following questions: (1) What are the relationships among the major subclades within Saxifragaceae, particularly within the heucheroids? (2) When did the major subclades of Saxifragaceae evolve, and was their evolution associated with specific geographic regions and/or geologic events? (3) What are the closest relatives of the enigmatic *Saniculiphyllum*?

2. Materials and methods

2.1. Taxon sampling and supermatrix assembly

We sampled 228 taxa, including 223 ingroup and 5 outgroup taxa, and included representatives of all genera of Saxifragaceae except the rare and monotypic *Hieronymusia* (suitable material not available), which is endemic to a small region of northern Argentina and southern Bolivia. It should be noted, however, that Gornall and Bohm (1985) considered *Hieronymusia* synonymous with *Suksdorfia* based on morphology and chemistry, a genus we did include here in our sampling. The Saxifragales genera *Itea* (Iteaceae), *Ribes* (Grossulariaceae), and *Liquidambar* (Altingiaceae) were selected as outgroups based on previous studies (Fishbein et al., 2001; Jian et al., 2008; Soltis et al., 2013; Soltis et al., 2001a).

Saxifragaceae have been the focus of numerous phylogenetic analyses (Holderegger and Abbott, 2003; Jian et al., 2008; Johnson and Soltis, 1995; Johnson et al., 1994; Kim and Kim, 2011; Morgan and Soltis, 1993; Okuyama et al., 2012; Oliver et al., 2006; Prieto et al., 2013; Reisch, 2008; Soltis and Soltis, 1997; Soltis et al., 2013; Soltis et al., 2001b; Soltis et al., 1996; Soltis et al., 1993; Vargas, 2000; Xiang et al., 2012; Xiang et al., 1998; Zhu et al., 2013), and many Saxifragaceae sequences are available on GenBank. We downloaded all available GenBank nucleotide sequences for Saxifragaceae as a starting point for our alignment. We then pruned or merged taxa in GenBank with synonymous names (e.g., *Bergenia cordifolia* = *Bergenia crassifolia*; *Saxifraga redofskyi* = *Saxifraga foliolosa*). Ultimately, we included only one sequence per species, keeping the longest sequence or the most recently added if sequences were the same length. All GenBank sequences were checked for accuracy by making phylogenetic trees for each individual gene region and checking the results against salient published results; sequences that seemed questionable/mislabeled were excluded from subsequent analyses. The GenBank contribution to our data alignment consisted of 2 nuclear and 11 plastid loci (Supplementary Appendix S1). As an initial data quality assessment check, we ran preliminary analyses using these GenBank data to identify any mislabeled or contaminant sequences and then removed such problematic sequences and loci.

Additionally, we obtained sequence data for 51 plastid loci and the 26S nuclear ribosomal region from the 1000 Plant Transcriptome Project (or 1KP Project; http://onekp.com/