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## Biogeography and diversification of Brassicales: A 103 million year tale

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## ABSTRACT

Brassicales is a diverse order perhaps most famous because it houses Brassicaceae and, its premier member, *Arabidopsis thaliana*. This widely distributed and species-rich lineage has been overlooked as a promising system to investigate patterns of disjunct distributions and diversification rates. We analyzed plastid and mitochondrial sequence data from five gene regions (>8000 bp) across 151 taxa to: (1) produce a chronogram for major lineages in Brassicales, including Brassicaceae and *Arabidopsis*, based on greater taxon sampling across the order and previously overlooked fossil evidence, (2) examine biogeographical ancestral range estimations and disjunct distributions in BioGeoBEARS, and (3) determine where shifts in species diversification occur using BAMM. The evolution and radiation of the Brassicales began 103 Mya and was linked to a series of inter-continental vicariant, long-distance dispersal, and land bridge migration events. North America appears to be a significant area for early stem lineages in the order. Shifts to Australia then African are evident at nodes near the core Brassicales, which diverged 68.5 Mya (HPD = 75.6–62.0). This estimated age combined with fossil evidence, indicates that some New World clades embedded amongst Old World relatives (e.g., New World capparoids) are the result of different long distance dispersal events, whereas others may be best explained by land bridge migration (e.g., *Forchhammeria*). Based on these analyses, the Brassicaceae crown group diverged in Europe/Northern Africa in the Eocene, circa 43.4 Mya (HPD = 46.6–40.3) and *Arabidopsis* separated from close congeners circa 10.4 Mya. These ages fall between divergent dates that were previously published, suggesting we are slowly converging on a robust age estimate for the family. Three significant shifts in species diversification are observed in the order: (1) 58 Mya at the crown of Capparaceae, Cleomaceae and Brassicaceae, (2) 38 Mya at the crown of Resedaceae + *Stixis* clade, and (3) 21 Mya at the crown of the tribes Brassiceae and Sisymbrieae within Brassicaceae.

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## 1. Introduction

Brassicales is a morphologically diverse lineage of ~4700 species placed in 18 families (APGIII, 2009) and united by the presence of mustard oils or glucosinolates (Table 1; Rodman et al., 1993, 1994, 1996, 1998). Variation in growth form, habitat occupied, floral and fruit features is so pronounced that these families were traditionally placed in seven orders across three different subclasses (e.g., Cronquist, 1981). Due to the evolution of this “mustard oil bomb” (Lüthy and Matile, 1984; Stauber et al., 2012) which involves glucosinolates and the accompanying

hydrolytic enzyme myrosinase often compartmentalized in special myrosin cells, the Brassicales have been a model group to evaluate the interplay of biochemical processes, natural selection involving deterring of herbivory, and myrosinase gene family evolution (Bekaert et al., 2012; Benderoth et al., 2006; Edger et al., 2015; Ehrlich and Raven, 1964; Hofberger et al., 2013; Prasad et al., 2012; Wheat et al., 2007; Wittstock et al., 2004). Because the largest family in the order, Brassicaceae, houses *Arabidopsis thaliana*, many studies focused on understanding the broader phylogenetic surroundings of this model plant (Hall et al., 2004; Rodman et al., 1993, 1996; Su et al., 2012). Examining the evolutionary development of flowers, for example, extends beyond studying *Arabidopsis*, and now involves explicit attempts to include the floral diversity portrayed by Brassicales (Bhide et al., 2014; Cheng et al., 2013; Patchell et al., 2011). Other economically important members are also in the order, such as papaya (*Carica papaya*, Caricaceae), mustard (*Brassica* and *Sinapis*, Brassicaceae), broccoli/cabbage/kale (*Brassica oleracea*, Brassicaceae), canola (*Brassica rapa*,

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**Table 1**

Members of the Brassicales including number of species, geographical range and sampling for this study.

Family	Genera/species (# in current study)	Geographical distribution
Akaniaceae	2/2 (2/2)	<i>Akania</i> – Australia <i>Bretschneidera</i> – Asia
Bataceae	1/2 (1/1)	Tropical America, Austral-Asia
Borthwickiaceae	1/1 (1/1)	China
Brassicaceae	338/3700 (26/35)	Cosmopolitan (mostly temperate)
Capparaceae	25/450 (23/49)	Cosmopolitan (mostly tropical)
Caricaceae	4/34 (1/1)	Tropical Africa and America
Cleomaceae	10/300 (8/29)	Cosmopolitan
Emblingiaceae	1/1 (1/1)	Southwest Australia
<i>Forchhammeria</i>	1/10 (1/3)	North and Central America
Gyrostemonaceae	5/18 (2/3)	Australia
Koerberliniaceae	1/1 (1/1)	North, Central, and South America
Limnanthaceae	2/10 (2/2)	North America
Moringaceae	1/13 (1/1)	Africa, Madagascar, and Asia
Pentadiplandraceae	1/1 (1/1)	Western Africa
Resedaceae	6/85 (5/8)	North Africa, Eurasia, North America
Salvadoraceae	3/12 (0/0)	Africa to Southeast Asia
Setchellanthaceae	1/1 (1/1)	North America
<i>Stixis</i>	1/7 (1/3)	India and Malaysia
<i>Tirania</i>	1/1 (1/1)	Southern Vietnam
Tovariaceae	1/2 (1/1)	Tropical America
Tropaeolaceae	3/92 (1/1)	North and South America

Brassicaceae), horseradish (*Armoracia rusticana*, Brassicaceae), caper (*Capparis spinosa*, Capparaceae), and moringa (*Moringa oleifera*, Moringaceae). Genomic resources abound with over 20 published genomes from the Brassicales (*Arabidopsis* Genome Initiative, 2000; Cheng et al., 2013; Dassanayake et al., 2011; Dorn et al., 2014; Edger et al., 2015; Haudry et al., 2013; Kagale et al., 2014a; Ming et al., 2008; Moghe et al., 2014; Slotte et al., 2013; Wang et al., 2011). The presence of at least three ancient whole genome duplications (WGD: reviewed in Barker et al., 2009; Franzke et al., 2011; Schranz and Mitchell-Olds, 2006; Schranz et al., 2006; Vision et al., 2000) makes the order a powerful system to investigate the role of WGD in angiosperm evolution (Schranz et al., 2012a,b).

Issues inherent in understanding the diversification of this order in form, time, and space are seen at many nodes in the emerging phylogenetic framework of Brassicales (Edger et al., 2015; Hall et al., 2004; Su et al., 2012). The woody Australasian Akaniaceae are sister to the mainly fleshy and scandent South American Tropaeolaceae, and these two families are then sister to all other families. The largely African Moringaceae (deciduous trees, shrubs, succulents) and South American Caricaceae (small trees or vines) are sister families and diverge next. The remainder of Brassicales is comprised of a group of five small families with uncertain relationships and a well-supported clade referred to as the “core Brassicales” (Hall et al., 2002, 2004; Rodman et al., 1996). The former includes the monotypic Setchellanthaceae (shrub from Mexico), the herbaceous Limnanthaceae from North America, the ditypic shrubby Koerberliniaceae from Mexico (and apparently having lost glucosinolates), and the closely related Bataceae (halophytic subshrubs) and Salvadoraceae (Old World shrubs or trees).

The core Brassicales contains two well-supported clades (Table 1; Hall et al., 2004; Su et al., 2012). The first comprises Capparaceae, Cleomaceae, and Brassicaceae, with the vast majority of species (~94%) within Brassicales placed in these three closely related families (Beilstein et al., 2010, and cited by others unfortunately restricted the term “core Brassicales” to only these three families). The second clade (hereafter referred to as “GRFT”) comprises Gyrostemonaceae, Borthwickiaceae, Resedaceae, and three anomalous genera, *Forchhammeria*, *Stixis*, and *Tirania*, currently

without family designation (Table 1; Hall et al., 2004; Su et al., 2012). The placements of African Pentadiplandraceae and Neotropical Tovariaceae relative to these two clades are less clear (Hall et al., 2004; Su et al., 2012). The Australian endemic Emblingiaceae is sister to all other core Brassicales.

Despite the presence of several species-rich clades within the Brassicales, explicit tests examining shifts in species diversification and/or extinction rates within the order have been limited in the context of a well-sampled phylogeny with appropriate fossil-based chronology and use of rate shift models that are allowed to vary through time in a diversity-dependent manner. Species diversification within Brassicales has been examined in the context of glucosinolate evolution and the corresponding coevolution of pierid cabbage butterflies, WGD, and the Cretaceous–Paleogene (K–Pg) event (previously referred to as the K–T event) (Beilstein et al., 2010; Benderoth et al., 2006; Edger et al., 2015; Prasad et al., 2012; Wheat et al., 2007), but many of these analyses used only limited taxon sampling and placeholders for most families. For example, the most recent study to date examining shifts in species diversification within Brassicales sampled 18 accessions from 14 of the 18 families, although this genomic approach did analyze 75,000 molecular characters (Edger et al., 2015). Moreover, the timing of such diversification events, whole genome duplications, glucosinolate evolution, the origin of *Arabidopsis thaliana* and close relatives is controversial because widely divergent dates exist for estimated ages within the order, especially Brassicaceae (Beilstein et al., 2010; Couvreur et al., 2010; Edger et al., 2015; Huang et al., 2016; Hohmann et al., 2015; Franzke et al., 2009, 2011).

No large-scale analysis of biogeographical relationships in the context of an age-structured phylogeny has been done, despite the fact that the apparent mid-Cretaceous age of the order (Bell et al., 2010; Magallón and Castillo, 2009; Magallón et al., 2015) and the widely distributed or strongly disjunct geographic patterns make this lineage an ideal system to investigate these phenomena. Of particular importance in Brassicales is the presence of multiple, intercontinental disjunctions, a pattern of intense biogeographical interest that has invoked vicariance or dispersal explanations (e.g., Antonelli et al., 2015; Axelrod, 1970; Berger et al., 2016; Buerki et al., 2011; Clayton et al., 2009; Cracraft, 1988; Crisp et al., 2011; Donoghue and Edwards, 2014; Givnish and Renner, 2004; Raven and Axelrod, 1974; Sanmartín and Ronquist, 2004; Spalink et al., in press, 2016; Sytsma et al., 2004, 2014). Within Brassicales, biogeographical analyses have been conducted within the amphiatlantic Caricaceae (Carvalho and Renner, 2012), cosmopolitan-distributed Cleomaceae (Feodorova et al., 2010), mainly Old World Resedaceae (Martín-Bravo et al., 2007, 2009), and Mexican Setchellanthaceae (Hernández-Hernández et al., 2013). These studies revealed complex patterns mostly driven by long-distance dispersal, which is consistent with some tropical amphiatlantic families (e.g., Bromeliaceae, Rapateaceae, Vochysiaceae; Berger et al., 2016; Givnish et al., 2000, 2004; Sytsma et al., 2004). However, other disjunct patterns in Brassicales may be explained by vicariance or by, often overlooked, intercontinental migration via four Northern Hemisphere land bridges (Brikiatis, 2014; Tiffney, 1985; Tiffney and Manchester, 2001; Wen, 1999). The more southerly Thulean North Atlantic Land Bridge (NALB) has been demonstrated to be important for other tropical families such as the Malpighiaceae, Fabaceae, and Rubiaceae (Davis et al., 2004; Christenhusz and Chase, 2013; Lavin and Luckow, 1993; Smedmark et al., 2010). Additional examinations in the Brassicales with multiple fossil calibrations are needed to identify whether long distance dispersal is the primary driving force in forming disjunct biogeographical patterns in the order.

In addition, we focus on two separate intercontinental disjunctions in the order that have yet to be investigated. First,

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