



## Dispersals of Hyoscyameae and Mandragoreae (Solanaceae) from the New World to Eurasia in the early Miocene and their biogeographic diversification within Eurasia

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### ABSTRACT

The cosmopolitan Solanaceae contains 21 tribes and has the greatest diversity in South America. Hyoscyameae and Mandragoreae are the only tribes of this family distributed exclusively in Eurasia with two centers of diversity: the Mediterranean–Turanian (MT) region and the Tibetan Plateau (TP). In this study, we examined the origins and biogeographical diversifications of the two tribes based on the phylogenetic framework and chronogram inferred from a combined data set of six plastid DNA regions (the *atpB* gene, the *ndhF* gene, the *rps16-trnK* intergenic spacer, the *rbcl* gene, the *trnC-psbM* region and the *psbA-trnH* intergenic spacer) with two fossil calibration points. Our data suggest that Hyoscyameae and Mandragoreae each forms a monophyletic group independently derived from different New World lineages in the early Miocene. Phylogenetic relationships within both tribes are generally well resolved. All genera of Hyoscyameae are found to be monophyletic and they diversified in middle to late Miocene. At nearly the same time, Mandragoreae split into two clades, corresponding to the MT region and the TP region, respectively. Both the phylogenetic relationships and the estimated ages of Hyoscyameae and Mandragoreae support two independent dispersal events of their ancestors from the New World into Eurasia. After their arrivals in Eurasia, the two tribes diversified primarily in the MT region and in the TP region via multiple biogeographic processes including vicariance, dispersal, recolonization or being preserved as relicts, from the mid Miocene to the late Quaternary.

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### 1. Introduction

The origin and evolution of disjunct distributions of organisms have long interested biogeographers (Manos and Donoghue, 2001; Raven and Axelrod, 1974; Thorne, 1972; Wen, 1999; Wen and Ickert-Bond, 2009; Wu, 1983). Vicariance became the prevailing explanation for many types of intercontinental disjunctions of plants and animals in the 1970s with the wide acceptance of the plate tectonics theory (Good, 1974; Nelson and Platnick, 1980; Sanmartin, 2003; Wiley, 1988). For example, the classical

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trans-Atlantic distributions of many plants have been considered associated with the breakup of Africa and South America (Raven and Axelrod, 1974; Wu et al., 2003). However, these two landmasses separated from each other 100–120 million years ago (mya) (Bauer, 1993; Hay et al., 1999), and vicariance may be appropriate only to interpret the distributions of some anciently diverged plant taxa, such as Annonaceae and Alstroemeriaceae – Luzuriagaceae, that were dated to Cretaceous (Doyle et al., 2004; Vinnersten and Bremer, 2001). Many plant taxa disjunct between Eurasia and North America may represent elements of the once continuous Arcto-Tertiary or boreal floras in the Tertiary (Li, 1952; Tiffney, 1985; Tiffney and Manchester, 2001). Nevertheless, these disjunctions from the breakup of the once continuous Arcto-Tertiary or boreal floras may be restricted to the mid-Tertiary temperate elements (such as *Anemone* of Ranunculaceae and *Viburnum* of Caprifoliaceae) or early Tertiary tropical elements (such as Illiciaceae), which adapted to the climatic conditions in the high-latitude regions of the northern hemisphere (Tiffney and Manchester, 2001; Wen, 1999, 2001). For taxa with tropical affinities and/or younger than Miocene, the vicariance hypothesis may not be plausible.

Recently, several molecular studies based on robust phylogenies and divergence time estimates suggest the importance of long-distance dispersal for some intercontinental disjunctions at the species or the genus level (Dick et al., 2007; Givnish et al., 2004; Nie et al., 2005; Schaefer et al., 2009; Wen and Ickert-Bond, 2009; Yokoyama et al., 1998). Long-distance dispersal between continents can be mediated by migratory animals, extreme meteorological phenomena, ocean currents, floating islands, or winds (Houle, 1998, 1999; Nathan et al., 2008; Renner, 2004; Winkworth et al., 2002). Ocean currents have been suggested for some taxa with trans-oceanic disjunctions, such as *Lathyrus* L. of Fabaceae (Kenicer et al., 2005), *Chrysosplenium* L. of Saxifragaceae (Soltis et al., 2001), and *Ceiba pentandra* L. of Malvaceae (Dick et al., 2007). Taxa with small propagules such as *Metrosideros* Banks ex Gaertn. of Myrtaceae (Wright et al., 2000), orchids (Carlquist, 1996; Winkworth et al., 2002) and ferns (McGlone et al., 2001) may disperse over long-distances via winds. *Lycium* L. (Solanaceae) has been suggested to be dispersed in a single event by birds from the New World to Eurasia followed by spreading into southern Africa (Fukuda et al., 2001; Levin and Miller, 2005). Long-distance dispersal has been also advocated as an explanation for the wide distribution of *Nicotiana* L. (Solanaceae) in the Americas, Australia and Africa (Aoki and Ito, 2000; Clarkson et al., 2004; Mummenhoff and Franzke, 2007).

Solanaceae is a cosmopolitan family with ca. 21 tribes, 100 genera and 2500 species (Hunziker, 2001; Olmstead and Bohs, 2007; Olmstead et al., 2008). This family has a center of diversity in the New World, particularly in South America (Hunziker, 2001). Hyoscyameae and Mandragoreae, however, are largely restricted to Eurasia, with only a few species of both tribes extending to northern Africa. The origins of the two Eurasian solanaceous tribes have been of interest to taxonomists and biogeographers, and different hypotheses were proposed regarding the formations of their current distributions. Lu and Zhang (1986) first analyzed the diversity and distribution of Hyoscyameae and noted that many genera and species occur in the Tibetan Plateau (TP) area, especially the mountains of the southeastern TP. They thus postulated its origin in the mountains of the southeastern TP. The Gondwanian origins of the two tribes, however, were postulated by some authors because most basal extant taxa of Solanaceae occur in the southern hemisphere (Hoare and Knapp, 1997; Symon, 1991; Tu et al., 2005; Ungricht et al., 1998). Based on the molecular phylogeny of Solanaceae and Solanales (Bremer et al., 2002; Olmstead et al., 2008; Stefanovic et al., 2002) and their overall distributions, Olmstead et al. (2008) suggested the New World as the most likely place of origin for the family with eight to nine minimum dispersal events into the Old World, which include the dispersals of Mandragoreae and Hyoscyameae.

Hyoscyameae contains eight genera and Mandragoreae is a monogeneric tribe with five species (Akhani and Ghorbani, 2003; Hoare and Knapp, 1997; Lu, 1997; Olmstead et al., 2008; Ungricht et al., 1998). Members of the two tribes are found throughout Eurasia but their distributions are often interrupted by deserts, steppes and mountains. The five mandrake species occur discontinuously in the Tibetan Plateau, the Turanian region, and the Mediterranean basin. Many genera of Hyoscyameae are isolated either in the Mediterranean–Turanian (MT) region (*Atropa* L., *Archihyoscyamus* A.M. Lu) or in the TP region (*Przewalskia* Maxim., *Anisodus* Link et Otto and *Atropanthe* Pascher). The two species of *Scopolia* are distributed disjunctly between eastern Asia and the Mediterranean basin. Overall two centers of diversity can be identified for both tribes: the MT region and the TP region. These two regions have been considered the most important 'hot spots' of biodiversity in Eurasia (Myers et al., 2000). Besides Hyoscyameae and Mandragoreae, many other unrelated taxa have similar distribution patterns in the two regions (see review by Sun, 2002). It has

been hypothesized that this distribution pattern among different Eurasian taxa could have been resulted from a common geologic or climatic event (Greuter, 1991; Jakob et al., 2007; Petit et al., 2003; Ribera and Blasco-Zumeta, 1998; Steward and Lister, 2001; Wu, 1988). Since the Cretaceous, the most remarkable physical changes of Eurasia were the retreat of Tethys Sea before Tertiary, the collision of the Indian Plate with Eurasia in early Tertiary followed by the uplift of the Himalayas and the aridification of Central Asia in the middle to late Tertiary, the connection and the breakup of Eurasia with North America through the Bering Land Bridge (BLB) and the North Atlantic Land Bridge (NALB) in the early to middle Tertiary, and the repeated advances/retreats of glaciers in the Quaternary (Barron and Peterson, 1989; Butler, 1995; Harrison et al., 1992; Lomolino et al., 2006; Tiffney and Manchester, 2001; Wen, 1999). However, the associations between the environmental changes and the distributions of plants throughout Eurasia have rarely been tested. Moreover, the physical events may not be the only option to explain the plants' distribution in Eurasia.

The explicit estimates of both phylogenies and ages of lineages are of critical importance in inferring the biogeographic histories of Hyoscyameae and Mandragoreae. Previous molecular phylogenetic studies on Solanaceae have shown that the Eurasian Hyoscyameae and Mandragoreae are nested within clades comprising groups endemic to or largely distributed in South America (such as Nolaneae, Lycieae, Physaleae and Solaneae) (Yuan et al., 2006; Olmstead et al., 2008), clearly suggesting the New World origin of these two tribes. However, the lack of information on their divergence times has hindered our understanding on whether the formation of the two intercontinental disjunctions was caused by dispersals from the New World to Eurasia, or by vicariance due to the breakup of the previously continuous distributions resulted from climate changes. More importantly their subsequent diversification within Eurasia needs to be analyzed based on a phylogenetic framework. In this study, we sampled seven of the eight genera from Hyoscyameae and all five species from Mandragoreae, and employed six plastid markers to infer a phylogeny. Using two fossils of Solanaceae as calibration points, we estimated the ages of the Old World–New World disjunctions, and the disjunctions within Eurasia. The phylogeny and the chronogram were then used to test the origins of the two tribes and to examine their biogeographic diversifications within Eurasia.

## 2. Materials and methods

### 2.1. Taxon sampling, DNA extraction, PCR, and sequencing

The sampling covered all five species of Mandragoreae and all eight genera of Hyoscyameae except the monotypic *Archihyoscyamus* A.M. Lu, which was previously placed in the genus *Hyoscyamus* (Hoare and Knapp, 1997; Lu, 1997). Due to the close relationships of the two tribes to Nolaneae, Lycieae, Jaboroseae, Physaleae and Solaneae from the subfamily Solanoideae (Olmstead et al., 2008), sequences from 15 samples of these tribes were also included in our phylogenetic analyses. Six plastid markers including the *atpB* gene, the *ndhF* gene, the *rps16-trnK* and the *psbA-trnH* intergenic spacer, the *rbcl* gene and the *trnC-psbM* region, were used to infer a phylogeny. The six markers were newly sequenced in this study or obtained from our recent study (Dillon et al., 2009). Two *Nicotiana* species (*N. sylvestris* Speg.; *N. tomentosiformis* Goodsp.) were used to root the tree. The taxa, the GenBank accession numbers, and the voucher information are presented in Table 1.

Total genomic DNA was extracted from silica gel-dried leaf materials following Tu et al. (2008) or from fresh leaves of transplanted individuals or of plants raised from seeds. The primers and PCR protocols for amplifying the six markers can be found in

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