



Molecular phylogeny of *Cissus* L. of Vitaceae (the grape family) and evolution of its pantropical intercontinental disjunctions

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ABSTRACT

Pantropical intercontinental disjunct distribution is a major biogeographic pattern in plants, and has been explained mainly by boreotropical migration via the North Atlantic land bridges (NALB) and transoceanic long-distance dispersal (LDD), and sometimes by vicariance. However, well-resolved phylogenies of pantropical clades are still relatively few. *Cissus* is the largest genus of the grape family Vitaceae and shows a pantropical intercontinental disjunction with its 300 species distributed in all major tropical regions. This study constructed the phylogenetic relationships and biogeographic diversification history of *Cissus*, employing five plastid markers (*rps16*, *trnL-F*, *atpB-rbcL*, *trnH-psbA* and *trnC-petN*). The results confirmed that *Cissus* polyphyletic, consisting of three main clades: the core *Cissus*, the *Cissus striata* complex, and the Australian–Neotropical disjunct *Cissus antarctica* – *C. trianae* clade. The latter two clades need to be removed from *Cissus* to maintain the monophyly of the genus. The core *Cissus* is inferred to have originated in Africa and is estimated to have diverged from its relatives in Vitaceae in the late Cretaceous. It diversified in Africa into several main lineages in the late Paleocene to the early Eocene, colonized Asia at least three times in the Miocene, and the Neotropics in the middle Eocene. The NALB seems the most plausible route for the core *Cissus* migration from Africa to the Neotropics in the middle Eocene. Three African–Asian and two Neotropical–Australian disjunctions in *Cissus* s.l. are estimated to have originated in the Miocene and may be best explained by LDD.

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1. Introduction

Pantropical intercontinental disjunct distribution is a major biogeographic pattern in plants (Thorne, 1972; Givnish and Renner, 2004; Bartish et al., 2011). Thorne (1972) documented that 334 genera and 59 families of seed plants show pantropical distributions in all major tropical regions of the world. Compared with the disjunct temperate floras in the Northern Hemisphere (Wen, 1998; Manos and Donoghue, 2001; Wen and Ickert-Bond, 2009; Wen et al., 2010), tropical intercontinental disjunctions remain poorly understood perhaps due to the greater species richness, the inaccessibility of the study material (Renner et al., 2001), the greater ocean gulfs, and the less dynamic latitudinal distributions of taxa (Givnish and Renner, 2004). Recent molecular phylogenetic studies combined with molecular clocks now allow a more precise understanding of the evolution of pantropical distributions in several vascular plant families and genera such as in Melastomataceae (Renner et al., 2001; Renner, 2004), Malpighiaceae (Davis et al., 2002, 2004), Annonaceae (Doyle et al., 2004; Richardson et al.,

2004; Erkens et al., 2009), Myristicaceae (Doyle et al., 2004), Burseraceae (Weeks et al., 2005), Moraceae (Zerega et al., 2005), Meliaceae (Muellner et al., 2006), Campanulaceae (Antonelli, 2009), Rubiaceae (Razafimandimbison et al., 2010; Smedmark et al., 2010), Simaroubaceae (Clayton et al., 2009), Sapotaceae (Bartish et al., 2011), and Diospyros (Duangjai et al., 2009).

Three hypotheses have been invoked to explain how the tropical/pantropical lineages evolved to occupy such a wide disjunct geographic range. With the acceptance of plate tectonics theory, vicariance was used to explain the wide distribution of lineages on the ancient Gondwana continent (Schönenberger and Conti, 2003; Thorne, 2004; de Queiroz, 2005). Vicariance as the biogeographic mechanism has been proposed in Annonaceae (Doyle and Le Thomas, 1997; Doyle et al., 2004) and Meliaceae (Muellner et al., 2006). The boreotropical migration hypothesis supports the migration of some tropical lineages with intercontinental disjunctions between the Old and the New World via the North Atlantic land bridges (NALB) during the early Tertiary, when climate conditions in the Northern Hemisphere accommodated a tropical vegetation (Davis et al., 2002, 2004). This hypothesis has been proposed to explain many lineages with a classical western Gondwanan disjunct pattern such as in Burseraceae (Weeks et al., 2005),

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Malpighiaceae (Davis et al., 2002, 2004), and *Gutteria* (Annonaceae, Erkens et al., 2009). The transoceanic long distance dispersal (LDD) has been commonly proposed, especially when divergence times of many lineages are far too young to implicate vicariance via tectonic plate movement (Davis et al., 2004; Thorne, 2004) or the NALB. Examples of LDD have been reported in Melastomataceae (Renner, 2004), Simaroubaceae (Clayton et al., 2009), and Chrysophylloideae (Sapotaceae, Bartish et al., 2011). Nevertheless, well-resolved phylogenies of pantropical clades are still relatively few (Clayton et al., 2009).

Cissus L. of Vitaceae (the grape family) shows a pantropical intercontinental disjunct pattern. *Cissus* contains approximately 300 species (Wen, 2007a) and represents the largest of the 14 genera of Vitaceae (Lombardi, 1997, 2007; Wen, 2007a; Wen et al., 2007). The genus has about 135 species in Africa, 85 species in Asia, 12 species in Australia, and 65 species in the Neotropics (Wen, 2007a). *Cissus* shows remarkable morphological diversity (Jackes, 1988; Lombardi, 2007), and is generally characterized by well-developed thick and undivided floral disks, four-merous flowers, one-seeded fruits, and seeds with a long and linear chalaza (Descouings, 1960; Wen, 2007a; Chen and Manchester, 2011). Jackes (1988) classified the Australian *Cissus* species into three groups. Lombardi (2007) placed the Neotropical *Cissus* species into 15 informal groups. The phylogenetic relationships of *Cissus* have been discussed in the context of Vitaceae phylogeny in several recent studies (Rossetto et al., 2001, 2002, 2007; Ingrouille et al., 2002; Soejima and Wen, 2006; Wen et al., 2007; Ren et al., 2011). These studies have shown that *Cissus* is polyphyletic, with most *Cissus* species belonging to a core clade; while four Neotropical *Cissus* (the *Cissus striata* complex) and four Australian *Cissus* (*C. antarctica* Vent., and its close relatives) did not form a clade with the core *Cissus*.

We herein expand the sampling scheme in *Cissus* and conduct phylogenetic, molecular dating, and biogeographic analyses to reconstruct the evolutionary diversification history of *Cissus* based on five plastid markers (*rps16*, *trnL-F*, *atpB-rbcL*, *trnH-psbA* and *trnC-petN*). Our sampling included taxa from all major tropical regions. The aims of this study are to: (1) reconstruct the *Cissus* phylogeny; (2) infer the ancestral area of *Cissus*; and (3) test competing hypotheses on the evolution of pantropical disjunctions.

2. Materials and methods

2.1. Sampling, DNA isolation and sequencing

The study sampled 174 accessions representing 117 accessions of *Cissus* (including 74 species) and 57 accessions (55 species) of related taxa of Vitaceae and Leeaceae (the sister family of Vitaceae; Wen, 2007b) and generated sequences for *trnL-F*, the *rps16* intron, *atpB-rbcL*, *trnH-psbA* and *trnC-petN* (Appendix Table A1). The sampling covered the geographic and morphological diversity of *Cissus*, with 16 species from Asia, 34 from Africa including Madagascar, 22 from the Neotropics, and two from Australia. We also included representatives of twelve other genera of Vitaceae in this study. Three *Leea* species (Leeaceae) were selected as outgroups.

Total DNAs were extracted from silica-gel-dried leaves or herbarium material by using a modified CTAB method (Doyle and Doyle, 1987) or the DNeasy Plant Mini Kit (Qiagen, Mississauga, Ontario, Canada) following the manufacturer's protocol. The *trnL-F* region was amplified and sequenced using primers c and f (Taberlet et al., 1991). When amplification of the *trnL-F* region was unsuccessful, we used primer combinations of c and d, and e and f (Taberlet et al., 1991; Soejima and Wen, 2006; Chen et al., 2011a). The *rps16* intron was amplified and sequenced using primers F and R2 (Oxelman et al., 1997; Andersons and Rova, 1999).

When primers F and R2 failed to sequence a few *Cissus* species, we used primer combinations of P3F (5'-TGC TCT TGG CTC GAC ATC G-3') and P2R (5'-GCG TTT CCT TGT TCC GGG-3'), and V1F (Chen et al., 2011a) and R2. The *atpB-rbcL*, *trnH-psbA* and *trnC-petN* regions were amplified and sequenced following Manen et al. (1994), Lee and Wen (2004), and Shaw et al. (2005), respectively. PCR products were purified with the polyethylene glycol (PEG) precipitation method (Wen et al., 2007). DNA sequences were assembled using the program Sequencher version 4.1.4 (Gene Codes Corp., Ann Arbor, Michigan, USA).

2.2. Sequence alignment and phylogenetic analysis

Sequence alignment was initially performed using the program MUSCLE 3.8.31 (Edgar, 2004) in multiple alignment routine, followed by manual adjustment with the program Se-AL version 2.0a11 (Rambaut, 2002).

Phylogenetic trees of the combined matrix of the five plastid DNA markers were reconstructed using maximum parsimony (MP, Fitch, 1971), maximum likelihood (ML) and Bayesian inference (BI) (Rannala and Yang, 1996; Mau et al., 1999). MP analyses were conducted under the heuristic search option using 10 random stepwise additions and tree-bisection-reconnection (TBR) branch swapping in PAUP* version 4.0 b10 (Swofford, 2003). Zero-length branches were collapsed and gaps were treated as missing data or coded as simple indels (Simmons and Ochoterena, 2000) using the program SeqState (Müller, 2005). Parsimony bootstrap analyses (Felsenstein, 1985) with 1000 replicates were subsequently performed under the option fast and stepwise addition to evaluate the robustness of the MP trees.

MrModeltest (Nylander, 2004) was used to determine the best available model for nucleotide substitutions. The generalized time reversible model (GTR + I + G model) was suggested as the best-fit model of sequence evolution for the combined plastid dataset. In the ML and BI analyses, we used the substitution models and parameters as estimated from MrModeltest.

Bayesian inference was used to estimate the posterior probabilities of phylogenetic trees by employing an analysis of five million generations Metropolis-coupled Markov chain Monte Carlo (MCMC) with MrBayes version 3.1.2 (Huelsenbeck and Ronquist, 2001). Different sequences were partitioned with unlinked substitution models as estimated before. The sampling rate of the trees was 1000 generations. The Bayesian trees sampled for the last four million generations were used to construct a 50%-majority rule consensus tree after discarding the first 10% samples as burn-in. The proportion of bifurcations found in this consensus tree was given as posterior clade probabilities (PP) as an estimator of the robustness of the BI trees.

2.3. Bayesian dating, fossil calibration

The combined *rps16*, *trnL-F*, *atpB-rbcL*, *trnH-psbA* and *trnC-petN* matrix was used to estimate the divergence times of clades. Representatives of *Cissus* from all main clades were sampled for the dating analyses with a fossil calibration. We largely followed the dating strategies in analyzing diversification of *Parthenocissus* (Nie et al., 2010) and *Ampelopsis* (Nie et al., 2012) of Vitaceae. The Program BEAST version 1.6.1 (Drummond and Rambaut, 2007) was used to date divergence times and employed a Bayesian relaxed clock model. After optimal operator adjustment as suggested by the output diagnostics from several preliminary BEAST runs, two final independent runs (each 50 million generations) were performed on a cluster of Mac XServes used for analysis of biological data at the Smithsonian Institution (<http://topazweb.si.edu>). Convergence between runs was assessed with MrBayes using Tracer version 1.5. After discarding the first 10%

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