

Phylogenetic position of *Dipentodon sinicus*: evidence from DNA sequences of chloroplast *rbcL*, nuclear ribosomal 18S, and mitochondria *matR* genes

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Abstract. Phylogenetic position of the monotypic genus *Dipentodon* has long been controversial. We investigated its position with 125 accessions representing 50 genera and 40 families of eudicots in the APG system. Four data sets—including the chloroplast gene *rbcL*, the nuclear 18S ribosomal DNA, and the mitochondrial gene *matR*, as well as the combined matrix—were used in the study with the maximum parsimony (MP) and Bayesian inference (BI) analyses. The phylogenetic trees based on individual genes and the combined data suggested that *Dipentodon* is sister to *Tapiscia* (Tapisciaceae) and that *Dipentodon* could be placed in eurosid II of the APG system. The clade of *Dipentodon* and *Tapiscia* is closest to Malvales and Sapindales. Such finding does not support the previously suggested close relationship between *Dipentodon* and various other groups, including Celastraceae, Samydaceae, Flacourtiaceae, Hamamelidaceae, and Santalales.

Keywords: Bayesian inference; Chloroplast *rbcL*; *Dipentodon sinicus*; Maximum parsimony; Mitochondrial *matR*; Molecular phylogeny; Nuclear ribosomal 18S.

Introduction

The genus *Dipentodon* Dunn consists of a single species *D. sinicus* Dunn, native to southern China and adjacent Burma and northeastern India (Merrill, 1941; Fischer, 1941; Li, 1986; Thorne, 1992; Bhattacharya and Johri, 1998). Its systematic position has been controversial since it was established and placed in the family Celastraceae in 1911 by S. T. Dunn. For example, Sprague (1925) moved it into the family Samydaceae based on the same variation range of floral base numbers in *Dipentodon* and Samydaceae. Many authors put the genus into the family Flacourtiaceae (including Samydaceae) (Fischer, 1941; Loesener, 1942; Metcalfe and Chalk, 1950; Lobreau, 1969). Record (1938) considered that *Dipentodon* is close to Hamamelidaceae based on the wood anatomic characters. Merrill (1941) proposed an independent family Dipentodontaceae Merr. and placed the family in Rosales between Hamamelidaceae and Rosaceae (Merrill, 1941;

Hutchinson, 1959, 1973; Schultze-Motel, 1964; Dahlgren, 1980; Cronquist, 1981; Takhtajan, 1987, 1997). However, Cronquist (1981) put the Dipentodontaceae into the order Santalales based on similar characters of the gynoeceal structure. In the update Angiosperm Phylogeny Group (APG) classification scheme of flowering plants, the phylogenetic position of Dipentodontaceae is still uncertain (Angiosperm Phylogeny Group, 1998; APG II, 2003).

Recently, DNA sequences of the chloroplast, nuclear ribosomal, and mitochondrial genes have been widely used in plant phylogenetics, especially in reconstructing angiosperm phylogeny (Hoot et al., 1995; Qiu et al., 1999; Soltis et al., 1998; Kuzoff and Gasser, 2000). More importantly, combining multiple genes from three genomes in plants has proved effective in reducing homoplasy generated by gene-, function-, and genome-specific molecular evolutionary phenomena (Qiu et al., 1999). However, phylogenetic information about *Dipentodon* is poorly known from molecular data. In the present paper, therefore, we conduct phylogenetic analyses of the *rbcL*, 18S, and *matR* sequences to determine the phylogenetic position of *Dipentodon* and its relationships with related groups.

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Materials and Methods

In-Group and Out-Groups

According to the APG classification scheme, 45 taxa for *rbcL*, 42 taxa for *matR*, and 31 taxa for 18S nrDNA, which represent the families Celastraceae, Samydeaceae, Flacourtiaceae, and others from the core eudicots were selected as the in-group. *Platanus occidentalis* (Platanaceae) and *Akebia quinata* (Lardizabalaceae) were selected as the out-groups for the phylogenetic analyses. GenBank accessions and the taxa used in this study are listed in Table 1.

DNA Extraction and Sequencing

Total genomic DNA was extracted from fresh and silica-gel-dried leaves using the CTAB procedure (Doyle and Doyle, 1987), and then purified with a DNA purification system (DPS) kit made by our laboratory. Aliquots of the total DNAs were used for sequencing all of the *matR* gene and part of *rbcL* and 18S rRNA genes. The PCR products of all samples were purified by using the QIAquick PCR Purification Kit (CN 28104, QIAGEN), and sequenced by using an ABI 377 Genetic Analyzer (Applied Biosystems, CA). All sequences have been deposited in GenBank (for accession numbers see Table 1).

Phylogenetic Analysis

The sequences used in this study were aligned with the Clustal-X program (Thompson et al., 1997) and modified manually. For phylogenetic analyses based on individual genes, the maximum parsimony (MP) method was used with PAUP* 4.0b5 (Swofford, 1999) (the heuristic search option with TBR branch-swapping and simple addition). Characters were assigned equal weights at all nucleotide positions (Fitch, 1971). Gaps were treated as missing data. Bootstrap analyses (Felsenstein, 1985) with 1000 replicates were performed to examine the relative level of support for individual clades on the phylogenetic trees. All phylogenetic trees were rooted using *Platanus occidentalis* and *Akebia quinata* as the out-groups.

A combined data set of the chloroplast, nuclear ribosomal, and mitochondrial sequences from 33 taxa was analyzed using the MP method implemented in the PAUP* 4.0b5 and the Bayesian inference (BI) method implemented in the MrBayes 2.0 (Huelsenbeck and Ronquist, 2001; Huelsenbeck et al., 2001). Since there was no topological difference between trees of the two out-groups and with either one out-group, *P. occidentalis* was selected as the out-group for the combined MP and BI analyses. MrBayes uses a MCMC algorithm that runs four Markov chains simultaneously. The Markov chains were started from a

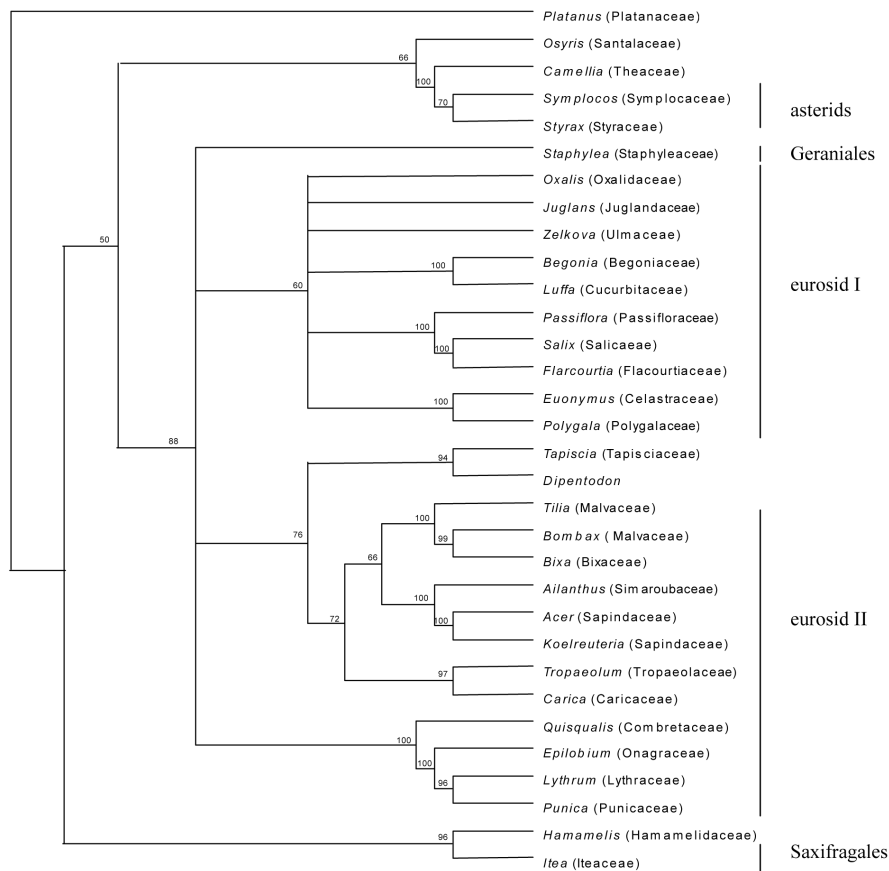


Figure 1. The most parsimonious tree (MPT) based on the combined data set. Numbers above branches represent the bootstrap values (%) for the clades with 1000 replicates. For tree parameters, see Table 2.

Table 1. GenBank accessions and the taxa sampled in this study. Classification based on APG (1998).

Family	Species	GenBank accession No		
		<i>matR</i>	<i>rbcL</i>	18S
EU DICOTS				
Lardizabalaceae	<i>Akebia quinata</i>	AF197810	L12627	L31795
Platanaceae	<i>Platanus occidentalis</i>	AF197793	L01943	U42794
CORE EU DICOTS				
Hamamelidaceae	<i>Hamamelis japonica</i>	*AF520087	L01922 (<i>H. mollis</i>)	AF015654
Iteaceae	<i>Itea yunnanensis</i>	*AF520099	AF190435 (<i>I. virginica</i>)	U42545 (<i>I. virginica</i>)
Santalaceae	<i>Osyris wightiana</i>	*AF520155	L11196 (<i>O. lanceolata</i>)	L24409 (<i>O. lanceolata</i>)
ROSIDS				
Geraniaceae	<i>Geranium wilfordii</i>	*AY121488	L14698 (<i>G. ocellatum</i>)	
Staphyleaceae	<i>Staphylea trifolia</i>	*AF520105	AJ238406	AJ235978
EUROSID I				
Begoniaceae	<i>Begonia laciniata</i>	*AY121500	U59814 (<i>B. ulmifolia</i>)	AF008950 (<i>B. oxyloba</i>)
Celastraceae	<i>Celastrus orbiculatus</i>	*AY121493		
Celastraceae	<i>Euonymus bungeanus</i>	*AY121492	L13184 (<i>E. alatus</i>)	X16600 (<i>E. alatus</i>)
Celastraceae	<i>Maytenus hookeri</i>		*AF499234	
Celastraceae	<i>Tripterygium hypoglaucum</i>		*AF499233	
Cephalotaceae	<i>Cephalotus follicularis</i>	*AF520193	L01894	
Cucurbitaceae	<i>Luffa cylindrica</i>	*AF520173	L21941 (<i>L. quinquefida</i>)	AF008957 (<i>L. quinquefida</i>)
Flacourtiaceae	<i>Flacourtia ramontchii</i>	*AF520186	*AF454736 (<i>F. montana</i>)	
Flacourtiaceae	<i>Homalium racemosa</i>		AJ418822	
Flacourtiaceae	<i>Poliothyrsis sinensis</i>		AJ402991	
Juglandaceae	<i>Juglans mandshurica</i>	*AF520073	U00437 (<i>J. nigra</i>)	AF206943 (<i>J. nigra</i>)
Oxalidaceae	<i>Oxalis corymbosa</i>	*AF520198	L01938 (<i>O. dillenii</i>)	AF206978 (<i>O. dillenii</i>)
Passifloraceae	<i>Passiflora edulis</i>	*AF520188	L01940 (<i>P. quadrangularis</i>)	AF206981 (<i>P. standleyi</i>)
Polygalaceae	<i>Polygala tatarinowii</i>	*AF520179	Z70176 (<i>P. chamaebuxus</i>)	U42797 (<i>P. pauciflora</i>)
Rhamnaceae	<i>Hovenia acerba</i>	*AF520156	AJ39039 (<i>H. dulcis</i>)	
Rhoipteleaceae	<i>Rhoiptelea chiliantha</i>	*AF520077	AF017687	
Rosaceae	<i>Prinsepia uniflora</i>	*AF520088	U06819 (<i>P. uniflora</i>)	
Salicaceae	<i>Salix raddeana</i>	*AF520191	AB012798 (<i>S. tetrasperma</i>)	AF207011 (<i>S. reticulata</i>)
Ulmaceae	<i>Celtis bungeana</i>	*AF520086	L12638	
Ulmaceae	<i>Zelkova serrata</i>	*AF520089	D86317	U42819
EUROSID II				
Bixaceae	<i>Bixa orellana</i>	*AF520136	Y15139	AF206868
Brassicaceae	<i>Capparis membranifolia</i>	*AF520146	M95754 (<i>C. hastata</i>)	
Bretschneideraceae	<i>Bretschneidera sinensis</i>	*AF520118	M95753	
Caricaceae	<i>Carica papaya</i>	*AF520141	M95671	U42514
Combretaceae	<i>Quisqualis indica</i>	*AF520133	L01948	AF207004
Lythraceae	<i>Lythrum salicaria</i>	*AF520110	L10218 (<i>L. hyssopifolia</i>)	AF206955
Malvaceae	<i>Bombax malabaricum</i>	*AF520148	AF022118 (<i>B. buonopozense</i>)	U42507 (<i>B. ceiba</i>)
Malvaceae	<i>Tilia mandshurica</i>	*AF520107	AF022127 (<i>T. americana</i>)	AF207042 (<i>T. americana</i>)
Onagraceae	<i>Epilobium hirsutum</i>	*AF520108	L10217 (<i>E. angustifolium</i>)	AF206907 (<i>E. angustifolium</i>)
Punicaceae	<i>Punica granatum</i>	*AY121502	L10223	U38311
Sapindaceae	<i>Acer mono</i>	*AF520112	L01881 (<i>A. saccharum</i>)	U42494 (<i>A. rubrum</i>)
Sapindaceae	<i>Koelreuteria bipinnata</i>	*AF520120	U39283 (<i>K. paniculata</i>)	AF206947 (<i>K. sp.</i>)
Simaroubaceae	<i>Ailanthus altissima</i>	*AF520106	L12566	AF206842
Tapisciaceae	<i>Tapiscia sinensis</i>	*AF520103	*AF447750, AF206825 (2)	AF207034
Tropaeolaceae	<i>Tropaeolum majus</i>	*AF520137	L14706	L28750
ASTERIDS				
Styracaceae	<i>Styrax grandiflorus</i>	*AF520205	AF396160 (<i>S. ramirezii</i>)	U43296 (<i>S. americana</i>)
EUASTERIDI				
Acanthaceae	<i>Blepharis hildebrandtii</i>	*AF520153	AF188127 (<i>Elytraria crenata</i>)	
Solanaceae	<i>Withania somnifera</i>	*AF520149	U08619 (<i>Schizanthus pinnatus</i>)	AF207016 (<i>S. pinnatus</i>)
Symplocaceae	<i>Symplocos setchuensis</i>	*AF520111	Z80193 (<i>S. ferruginea</i>)	U43297 (<i>S. paniculata</i>)
Theaceae	<i>Camellia sp.</i>	*AF520203	L12602 (<i>C. japonica</i>)	U42815 (<i>C. japonica</i>)
FAMILIES OF UNCERTAIN POSITION				
Dipentodontaceae	<i>Dipentodon sinicus</i>	*AY121494	*AF375609	*AF375610

*Represent the samples which were sequenced in this study.

random tree and run for 100,000 generations sampling every 50 generations for a total of 2,000 samples each run. The first 100 samples from each run were discarded as burn-in. The gamma distribution (Yang, 1994) and HKY model (Hasegawa et al., 1985) were used in the BI analysis.

Results and Discussion

After sequence alignment, four data sets were formed for phylogenetic analyses: 1) the chloroplast *rbcL* data set containing 48 taxa was 1,382 bp in length; 2) the nuclear ribosomal 18S data set containing 33 taxa was 1,734 bp; 3) the mitochondrial *matR* data set containing 44 taxa was

1,549 bp; and 4) the combined data set containing 33 taxa was 4,537 bp. The parameters of the most parsimonious trees (MPTs) obtained from the four data sets are presented in Table 2.

The strict consensus trees of the MPTs based on the individual and combined data sets showed a congruent topology. In the combined tree (Figure 1), *Dipentodon sinicus* is shown to be sister to *Tapiscia sinensis* (Tapisciaceae), with a relatively high bootstrap support value (95%).

The BI tree based on the combined data set is shown in Figure 2. The sister group relationship between *D. sinicus* and *T. sinensis* is strongly supported with a high

Table 2. Comparison of indices for the various trees analyzed using MP in this study, Consistency index (CI) excludes uninformative characters, RI = retention index, RC = rescaled consistency index.

Data set (OTUs)	No. variable characters (%)	No. informative characters (%)	No. of trees	Length of trees	CI	RI	RC	Bootstrap support (%)*
<i>matR</i> (44)	521 (33.6%)	230 (14.8%)	307	869	0.5566	0.6200	0.4495	<50
<i>rbcL</i> (48)	496 (34.6%)	323 (23.4%)	4	1707	0.3282	0.4813	0.1957	66
18S (33)	272 (15.6%)	146 (8.4%)	1	681	0.3720	0.4825	0.2400	<50
<i>matR/rbcL/18S</i> (32)	1104 (24.3%)	587 (12.6%)	2	2584	0.5329	0.4570	0.2436	76

*For the clade, *Tapiscia*+*Dipentodon* and the Sapindales, Malvaceae and Brassiclaes.

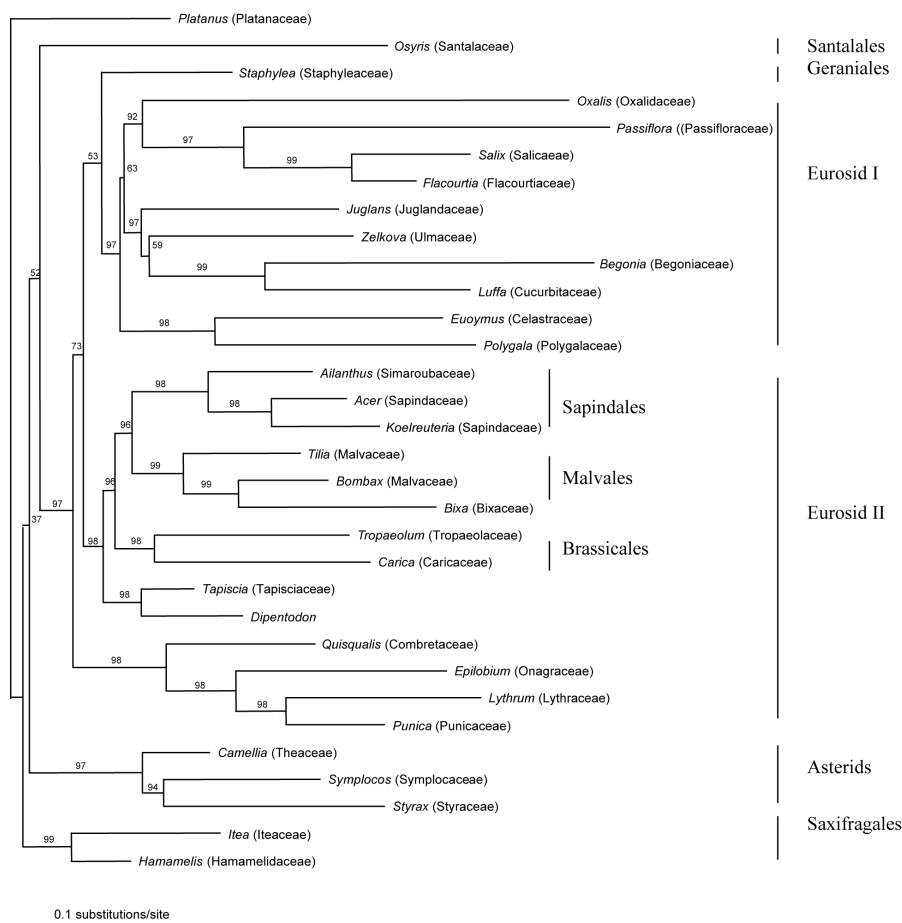


Figure 2. Phylogenetic tree determined by Bayesian Inference from the combined data set. Numbers above branches represent Posterior probabilities (PP). (HKY85 model: $K_a=3.12$).

posterior probability (PP = 0.98). The two species are then sister to the clade consisting of three orders: Malvales, Sapindales, and Brassicales with the same posterior probability support (PP = 0.98). The clade, which can be identified as the eurosid II in APG, is also shown to be sister to the clade consisting of the eurosid I clade and the genus *Staphylea*. Within the eurosid I clade, the sister group relationship between the families Flacourtiaceae and Celastraceae is well supported (PP = 0.97).

Based on the small number of genera sampled, our study suggests that the genus *Tapiscia* is most closely related to *Dipentodon*. The genus *Tapiscia* was established by Oliver (1890) and placed in the family Sapindaceae. However, it has been placed in the family Staphyleaceae by many authors (Diels, 1909; Bean, 1909; Schneider, 1912; Cronquist, 1981) and recognized as a distinct family by Takhtajan (1987). In the APG system, the family Tapisciaceae has not been assigned to any order but at the base of the “eurosid II” (APG, 1998). Simmons et al. (1998) indicated that the data from *rbcL* and ITS sequences suggested a different ordinal placement for *Huertia* and *Tapiscia* from other members of Staphyleaceae.

Our study also shows that the clade *Dipentodon* and *Tapiscia* and that of Malvales and Sapindales form a sister group. This does not support a close relationship of *Dipentodon* to any of the families to which it traditionally been considered closely related. Tapisciaceae are also shown to have a distant relationship to Staphyleaceae. However, there are relatively low bootstrap values at some deeper nodes. In general, the results obtained from the three different genes mostly agree with the treatments about those families in APG system (APG, 1998).

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十齒花 (*Dipentodon sinicus*) 的系統位置—來自葉綠體 *rbcL*、核糖體 18S 和線粒體 *matR* 基因的 DNA 序列證據

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十齒花科 (Dipentodontaceae) 在目前流行的有花植物分類系統 (APG) 中屬於位置未定的類群。本文採用 PCR 和自動測序的方法獲得十齒花 (*Dipentodon sinicus*) 及若干相關類群的葉綠體 *rbcL*、核糖體 18S 和線粒體 *matR* 基因的 DNA 序列。應用最大簡約法和貝葉斯推斷法，對自測序列和 GenBank 下載序列組成的資料矩陣進行單基因和三基因聯合的分支分析及統計檢驗。結果表明：十齒花與銀鵝樹構成姐妹群，二者構成的分支與錦葵目和無患子目關係較近，不支持前人認為與衛矛科、天料目科、大風子科、金縷梅科以及檀香目等親緣關係較近的觀點。

關鍵詞：十齒花；分子系統發育；最大簡約法；貝葉斯推斷法；葉綠體 *rbcL* 基因；核糖體 18S 基因；線粒體 *matR* 基因。