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Phylogeny of *Catalpa* (Bignoniaceae) inferred from sequences of chloroplast *ndhF* and nuclear ribosomal DNA

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Abstract Phylogenetics of *Chilopsis* and *Catalpa* (Bignoniaceae) was elucidated based on sequences of chloroplast *ndhF* and the nrDNA ITS region. In Bignoniaceae, *Chilopsis* and *Catalpa* are most closely related as sister genera. Our data supported section *Macrocatalpa* of the West Indies and section *Catalpa* of eastern Asian and North American continents. Within section *Catalpa*, *Catalpa ovata* of eastern Asia form a clade with North American species, *C. speciosa* and *C. bignonioides*, while the other eastern Asian species comprise a clade where *C. duclouxii* is sister to the clade of *C. bungei* and *C. fargesii*. The Caribbean species of *Catalpa* diverged early from the continental species. More studies are needed to test whether the phylogenetic pattern is common in eastern Asian-North American disjunct genera with species in the West Indies.

Key words Bignoniaceae, *Catalpa,* eastern Asia-North America, *ndhF* gene, nrDNA ITS sequences, phylogeny, West Indies.

Catalpa Scop. (Bignoniaceae), an intercontinental disjunct genus, consists of ten species, with two species in eastern North America (ENA), four in eastern Asia (EAS), and four in the West Indies (WI) (Li, 1952; Paclt, 1952; Gentry, 1992). Species of *Catalpa* are semievergreen or deciduous trees with opposite or whorled leaves. Their bisexual flowers are arranged in a raceme or panicle, and have two fertile stamens, a 2-lipped corolla, and tetrad pollen grains (Gentry, 1992). Four semievergreen species of section *Macrocatalpa* Griseb. are distributed in the WI, including *C. brevipes* Urban, *C. longissima* Sims, *C. macrocarpa* Ekman, and *C. purpurea* Griseb. (Manning, 2000). Species of section *Catalpa* are deciduous and disjunctly distributed between EAS and ENA. *Catalpa bignonioides* Walter, or the southern catalpa, has an original distribution in northern Florida and southwestern Georgia to southern Alabama and eastern Mississippi (Duncan & Duncan, 1988), Louisiana (Little, 1979), or easternmost Texas (Weniger, 1996). *Catalpa speciosa* Warder ex Engelm., the western catalpa, is native to the Mississippi River drainage basin from central Illinois and Indiana to northeastern Arkansas, western Tennessee (Beillman 1946; Little, 1979), and Louisiana (Burk & McMaster, 1988; Duncan & Duncan, 1988; Thomas & Allen, 1996). Both species have spread to other areas as a result of their cultivation as garden or lawn trees (Beillmann, 1946). *Catalpa ovata* G. Don is distributed in central and northern China. Its young leaves are edible, while the extract of mature leaves and barks has been used as pesticide and in traditional Chinese medicine (Wang, 1990). *Catalpa bungei* C. A. Mey. and *C. fargesii* Bureau are distributed in central to southwestern China, and the latter has a glabrous form, namely, *C. fargesii* f. *duclouxii* (Don) Gilmour (Gilmour, 1936; =*C. duclouxii* Dode). *Catalpa tibetica* Forrest is endemic to southwestern China and shares creamy-yellow flowers with *C. ovata* (Forrest, 1921).

Catalpa shares many reproductive characters with *Chilopsis* D. Don, a monotypic genus of the Chihuahuan and Sonoran deserts of northern Mexico and the southwestern United States (Henrickson, 1985; Gentry, 1992). Sterile hybrids have also been formed between *Catalpa* species and *Chilopsis linearis* Sweet (Rusanov, 1964; Li et al., 2006). Therefore, *Catalpa* has been considered as most closely related to *Chilopsis* in Bignoniaceae (Gentry, 1992).

In this study, interspecific relationships of *Catalpa* were estimated based on sequences of chloroplast gene *ndhF* and the internal transcribed spacers of nuclear ribosomal DNA (nrDNA ITS). Both DNA regions have been widely used for resolving lower level relationships of plant groups (Baldwin et al., 1995; Soltis et al., 1998; Davis et al., 2002). Specifically, I focused on the following three questions: (1) Are *Chilopsis* and *Catalpa* most closely related genera in Bignoniaceae? (2) Are sections *Macrocatalpa* and *Catalpa* each monophyletic? (3) Are North American

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species more closely related to the West Indian species or eastern Asian species?

1 Material and Methods

1.1 Taxon sampling

Thirteen samples of *Catalpa* and *Chilopsis* were included representing all species of the two genera except for *Catalpa brevipes*, *C. purpurea*, and *C. tibetica*, whose materials were unavailable for molecular study. Previous studies have recognized the monophyly of Bignoniaceae (Spangler & Olmstead, 1999; Olmstead et al., 2000). Nevertheless, the phylogenetic relationships of *Chilopsis* and *Catalpa* with other genera of the family remain unclear. Therefore, I also included 18 other bignoniaceous genera representing all tribes of the Bignoniaceae (Spangler & Olmstead, 1999) and their *ndhF* sequences were obtained from the GenBank (Table 1).

1.2 Molecular techniques

DNAs were extracted from silica-gel dried or fresh leaf tissue using a Qiagen DNeasy Plant Mini Kit (cat. # 69104, Germantown, MD). The nrDNA ITS region was amplified using primers ITS4 (White et al., 1990) and ITSLeu (Baum et al., 1998). A 25 μL PCR reaction included 2.5 μL *Taq* polymerase buffer (10 ×), 4 μL of dNTP (2.5 mmol/L), 2 μL of $MgCl_2$ (25 mmol/L), 1 μL of each primer (10 μmol/L), 0.2 μL of *Taq* polymerase (5 U/μL), 50–100 ng DNA, 2 μL of DMSO (dimethyl sulfoxide), and an appropriate amount of sterilized water. The thermocycler program consisted of the following steps: a hot-start of 94 ℃ for 3 min, 35 cycles of 94 ℃ for 1 min, 55 ℃ for 2 min, and 72 ℃ for 1 min. The final cycle was followed by an additional 7 min extension at 72 ℃. The amplified products were purified using a Qiagen Gel Purification Kit (Santa Clarita, CA).

The 3′ end segment of the *ndhF* gene was amplified in an MJ-PT200 Thermocycler using primers *ndhF*972F and 2210R (Olmstead & Sweere, 1994). A 25 μL reaction contained 50–100 ng of genomic DNA, 4 μL of DNTPs (2.5 mmol/L), 3 μL of $MgCl_2$, 2.5 μL of *Taq* polymerase buffer (10 ×), 0.3 μL of *Taq* polymerase (5 U/μL), 1 μL of each primer (10 μmol/L), and sterilized water. The PCR program consisted of a 3 min hot-start at 94 ℃ and 35 cycles of 1 min denature at 94 ℃, 1.5 min annealing at 50 ℃, and 2 min extension at 72 ℃. The cycles were followed by an additional 7 min extension at 72 ℃. Our initial attempt to do direct sequencing of the PCR products failed, indicating that there might be sequence polymorphisms in species of *Catalpa* and *Chilopsis*. Therefore, the PCR products were cloned using a standard p^{GEM} T Easy Vector System (Promega, Madison). From the same species more than one accession was sampled to detect for intraspecific variation and for each accession three to eight clones were sequenced. Repeated DNA extraction, PCR, and sequencing reactions were conducted to detect PCR errors that may have led to sequence variation. Clones and PCR products were sequenced using the Dideoxy Terminator Chemistry with an ABI BigDye Cycle Sequencing Ready Reaction kit. Sequences were analyzed using an ABI 3100 or 3730 Genetic Analyzer, and were edited using Sequencher (Version 4.1, GeneCode Inc., Ann Arbor, MI).

1.3 Phylogenetic analyses

In all phylogenetic analyses, characters were weighted equally and their state changes were treated as unordered. Gaps in sequences were treated as missing data. Sequences of both *ndhF* and nrDNA ITS regions were aligned readily by sight. Phylogenetic analyses were conducted using Maximum parsimony (MP) and maximum likelihood (ML) methods in PAUP* (Swofford, 2002). Heuristic tree search in MP analyses included the following options: 1000 replicates of random sequence addition with 1 tree held each replicate, TBR branch swapping, Multrees on, and steepest descent off. Branch and bound tree search was conducted using default options in PAUP*. Bootstrap analyses of 1000 replicates (Felsenstein, 1985) were carried out to estimate support for individual clades using options as in parsimony analyses with heuristic tree search except for simple sequence addition. Modeltest (version 3.06, Posada & Crandall, 1998) was used to select the best model for molecular data sets. Then, the estimated parameters of the selected model were applied in the ML analyses. The congruence of the nrDNA ITS and *ndhF* data sets was evaluated by comparing tree topologies from individual data sets to check whether there are well-supported (bootstrap support, bs>70%) but conflicting clades.

2 Results

2.1 Sequence characteristics

The 3′ portion of the *ndhF* gene and the entire nrDNA ITS region were newly obtained from the thirteen accessions of *Chilopsis* and *Catalpa* and the sequences have been submitted to GenBank (Table 1). The segment of the *ndhF* gene corresponded to the region between positions 1011–2096 of the *ndhF* gene in *Campsis radicans* (AF102626) and was 1086 base

Table 1 Species included in the study

Species	Source and voucher	GenBank Accessions	
		ndhF	nrDNA ITS
Arrabidaea pubescens (L.) A. H. Gentry	–	AF102625	–
Amphitecna apiculata A. H. Gentry	–	AF102624	–
Campsis radicans (L.) Seem.	–	AF102626	–
Crescentia portoricensis Britton	–	AF10262	–
Cybistax donnell-smithii (Rose) Seibert	–	AF102628	–
Cydista aequinoctialis Miers	–	AF102629	–
Eccremocarpus scaber Ruiz & Pav.	–	AF102630	–
Jacaranda sparrei A. H. Gentry	–	AF102631	–
Kigelia africana (Lam.) Benth.	–	AF102632	–
Macfadyena unguis-cati (L.) A. H. Gentry	–	AF102633	–
Martinella obovata Bureau & K. Schum.	–	MAXCPNDH	–
Ophiocolea floribunda (Boj. ex Lindl.) H. Perrier	–	AF102634	–
Oroxylum indicum (L.) Benth. ex Kurz	–	AF102635	–
Podranea ricasoliana Sprague	–	AF102637	–
Radermachera frondosa Chun & F. C. How	–	AF102638	–
Tabebuia heterophylla (DC.) Britton	–	TABCPNDH	–
Pandorea jasminoides Schum.	–	AF102636	–
Tecoma stans Juss.	–	AF130145	–
Chilopsis linearis Sweet	Genhua Niu, Texas A & M Univ., jli4196	**DQ411419**	**AY178657**
Catalpa longissima Sims	FBG 961378*A, jli3181	**DQ411414**	**AY486294**
Catalpa macrocarpa Ekman	FBG 66346*A, jli3182	**DQ411415**	**AY486295**
Catalpa duclouxii Dode 1	AA 642-94A, jli3233	**DQ411418**	**AY486296**
Catalpa duclouxii 2	FM Jun Wen 5705, jli3250	**DQ411417**	**AY486297**
Catalpa bungei C. A. Mey.	AA 12927A, jli3221	**DQ411410**	**AY486299**
Catalpa fargesii Bureau	AA 12222B, jli3211	**DQ411411**	**AY486300**
Catalpa ovata G. Don 1	AA 516-87A, jli3212	**DQ411412**	**AY486302**
Catalpa ovata 2	AA 98-61A, jli3214	**DQ411413**	**AY486303**
Catalpa speciosa Warder ex Engelm. 1	AA 1245-79C, jli3210	**DQ411408**	**AY486305**
Catalpa speciosa 2	AA 927-58B, jli3209	**DQ411409**	**AY486306**
Catalpa speciosa 3	AA 131-54A, jli3230	**DQ411407**	**AY486307**
Catalpa bignonioides Walter	AA 592-60C, jli3237	**DQ411416**	**AY486308**

AA, Arnold Arboretum accessions with wild provenance; FBG, Fairchild Botanical Gardens; FM, Field Museum at Chicago; sequences newly obtained are highlighted in bold.

pairs (bp) in all genera of Bignoniaceae. There were 305 variable sites, 115 of which were parsimony informative (10.6%). Some *ndhF* clones of *Catalpa* and *Chilopsis* were pseudogenes as indicated by frameshift indels and base mutations, and premature codons (Li et al., unpublished data). However, such pseudogenes were not available from *Catalpa longissima* or *C. macrocarpa*. Thus, they were excluded from phylogenetic analysis.

Sequence heterogeneity of the nrDNA ITS region within species was not observed in any of the taxa sampled. Sequence length ranged from 617–631 bp in *Catalpa* and *Chilopsis*. The GC content was ca. 61% and did not differ significantly, as judged by the Chi-square test of homogeneity of base frequencies across the taxa in PAUP*. Sequence divergence ranged from 7.4%–8.7% between *Chilopsis linearis* and *Catalpa* and from 6.4%–8.3% between sections *Macrocatalpa* and *Catalpa*. Within sections sequence divergence ranged from 0.2%–5.8%. The sequence alignment of nrDNA ITS region generated a data set of 634 sites, requiring 9 single base gaps. There were 95 variable sites, 66 of which were parsimony informative.

2.2 Phylogenetic relationships

2.2.1 *ndhF* data Parsimony analyses of *ndhF* gene sequence data generated 14 trees in one island of 441 steps. Figure 1 is the strict consensus rooted with *Jacaranda sparrei* A. H. Gentry and *Podranea ricasoliana* Sprague (*CI*=0.82, *RI*=0.79). There were six major branches: (1) *Eccremocarpus scaber* Ruiz & Pav.; (2) *Pandorea jasminoides* Schum., *Tecoma stans* Juss., and *Campsis radicans* (L.) Seem.; (3) *Amphitecna apiculata* A. H. Gentry, *Crescentia portoricensis* Britton, *Cybistax donnell-smithii* (Rose) Seibert, *Tabebuia heterophylla* (DC.) Britton, *Kigelia africana* (Lam.) Benth., *Ophiocolea floribunda* (Boj. ex Lindl.) H. Perrier, and *Radermachera frondosa* Chun & F. C. How (bs=60%); (4) *Arrabidaea pubescens* (L.) A. H. Gentry, *Martinella obovata* Bureau & K. Schum., *Macfadyena unguis-cati* (L.) A. H. Gentry, and *Cydista aequinoctialis* Miers (bs=100%); (5) *Oroxylum indicum* (L.) Benth. ex Kurz; and (6) *Chilopsis* and *Catalpa* (bs=96%). However, relationships among these clades were not resolved. *Chilopsis* was sister to *Catalpa*, whose species formed a strongly supported clade (bs=100%). Within *Catalpa*, there were two clades corresponding to sections *Macrocatalpa* (bs=100%) and *Catalpa* (bs=94%). Section *Catalpa* had three branches whose relationships were not resolved. North American species, *C. speciosa* and *C. bignonioides*, formed a clade (bs=99%). Three Asian species also formed a clade including *C. duclouxii*, *C. bungei*, and *C. fargesii*. However, *C. ovata*, another Asian species, did not cluster with either of the previous clades.

Modeltest selected GTR+G as the best model of evolution for *ndhF* sequences and the estimated parameters were as follows: base frequencies (A=0.3079, C=0.1459, G=0.1697, T=0.3764), rate matrix (A-C=2.0086, A-G=2.6265, A-T=0.1926, C-G=2.467, C-T=2.6265, G-T=1), and Gamma shape parameter=0.8248. ML analyses using the estimated parameters produced a single tree with a likelihood of –ln=4057.8275. The ML tree topology (not shown) suggested the same relationships of *Chilopsis* and *Catalpa* as in the parsimony tree (Fig. 1).

2.2.2 nrDNA ITS region The ITS data set contained 13 samples of *Chilopsis* and *Catalpa* because our *ndhF* data strongly support the sister relationship of the two genera (see above). Furthermore, this relationship has long been suggested based on morphological evidence (Gentry, 1992). Parsimony analyses of the 13-taxon data set using branch and bound tree search produced 3 trees of 117 steps, one of which is shown in Fig. 2a (*CI*=0.88, *RI*=0.92). Sections *Macrocatalpa* and *Catalpa* each formed their own clades (bs=100% and 92%, respectively). Within section *Catalpa* there were two clades, including (*C. ovata*, (*C. speciosa*, *C. bignonioides*)) and (*C. duclouxii*, (*C. bungei*, *C. fargesii*)). All clades were strongly supported. ML analyses were performed using the HKY+G model selected by Modeltest and the estimated parameters included base frequencies (A=0.1915, C=0.3105, G=0.2899, T=0.2082), Ti/Tv ratio=2.57, and Gamma shape parameter=0.1971. The ML tree with a likelihood of –ln=1513.9849 was entirely congruent with Fig. 2a except that three accessions of *C. speciosa* formed a moderately supported clade (bs=75%, Fig. 2b).

2.2.3 *ndhF*+nrDNA ITS Phylogenetic trees inferred from the *ndhF* gene (Fig. 1) and nrDNA ITS (Fig. 2) were congruent. Therefore, the two data sets were combined resulting in a matrix of 1720 sites. Parsimony analyses using branch and bound tree search generated 3 tree of 173 steps (*CI*=0.91, *RI*=0.93). These trees differed in the relationships of the three accessions of *C. speciosa* to *C. bignonioides*. The consensus tree (not shown) was congruent with the ITS tree (Fig. 2) with higher bootstrap support for all clades.

3 Discussion

Catalpa and *Chilopsis* are nearly identical in fruit, seed, embryo, style, and anther characteristics (Gentry, 1980; Henrickson, 1985; Manning, 2000). They share pollen tetrads with sculpturing limited to coarsely reticulate areoles, a unique pollen type in the Bignoniaceae (Gentry & Tomb, 1979). In addition, an intergeneric sterile hybrid has been reported between *Catalpa* and *Chilopsis* (Rusanov, 1964) and has recently been confirmed based on molecular data (Li et al., 2006). *Chilopsis* is sister to the clade containing all species of *Catalpa*, offering strong support for the close affinity of the two genera (Fig. 1).

Catalpa has been divided into sections *Macrocatalpa* and *Catalpa* (Paclt, 1952; Gentry 1980, 1992; Manning, 2000). In the nrDNA ITS, chloroplast *ndhF* gene, and combined trees (Figs. 1, 2), the two species of section *Macrocatalpa* form a robust clade, so do species of section *Catalpa*. Their monophyly also gets support from morphology. For example, leaves are elliptic and evergreen in section *Macrocatalpa* (vs. broadly ovate and deciduous in section *Catalpa*) (Paclt, 1952). Foliar nectaries occur at basal junction of primary and secondary veins in section *Macrocatalpa* (vs. at basal junction and along the midveins

in section *Catalpa*). Trichomes are scale-like in section *Macrocatalpa* (vs. global in section *Catalpa*). Seeds are fimbriate all around in section *Macrocatalpa* (vs. fimbriate terminally in section *Catalpa*) (Elias & Newcombe, 1979). Britton (1918) elevated section *Macrocatalpa* to the genus level based on leaf morphology and geographic distribution. However, because the two sections are each monophyletic and are sister to each other, it is a matter of personal preference whether or not to recognize *Macrocatalpa* as a separate genus (Stevens, 1997). Here I adopt the general view, recognizing them as sections *Macrocatalpa* and *Catalpa*.

Within section *Catalpa*, the two North American species have been suggested to be conspecific (Warder, 1881; Roberts, 1902; Manning, 2000). They

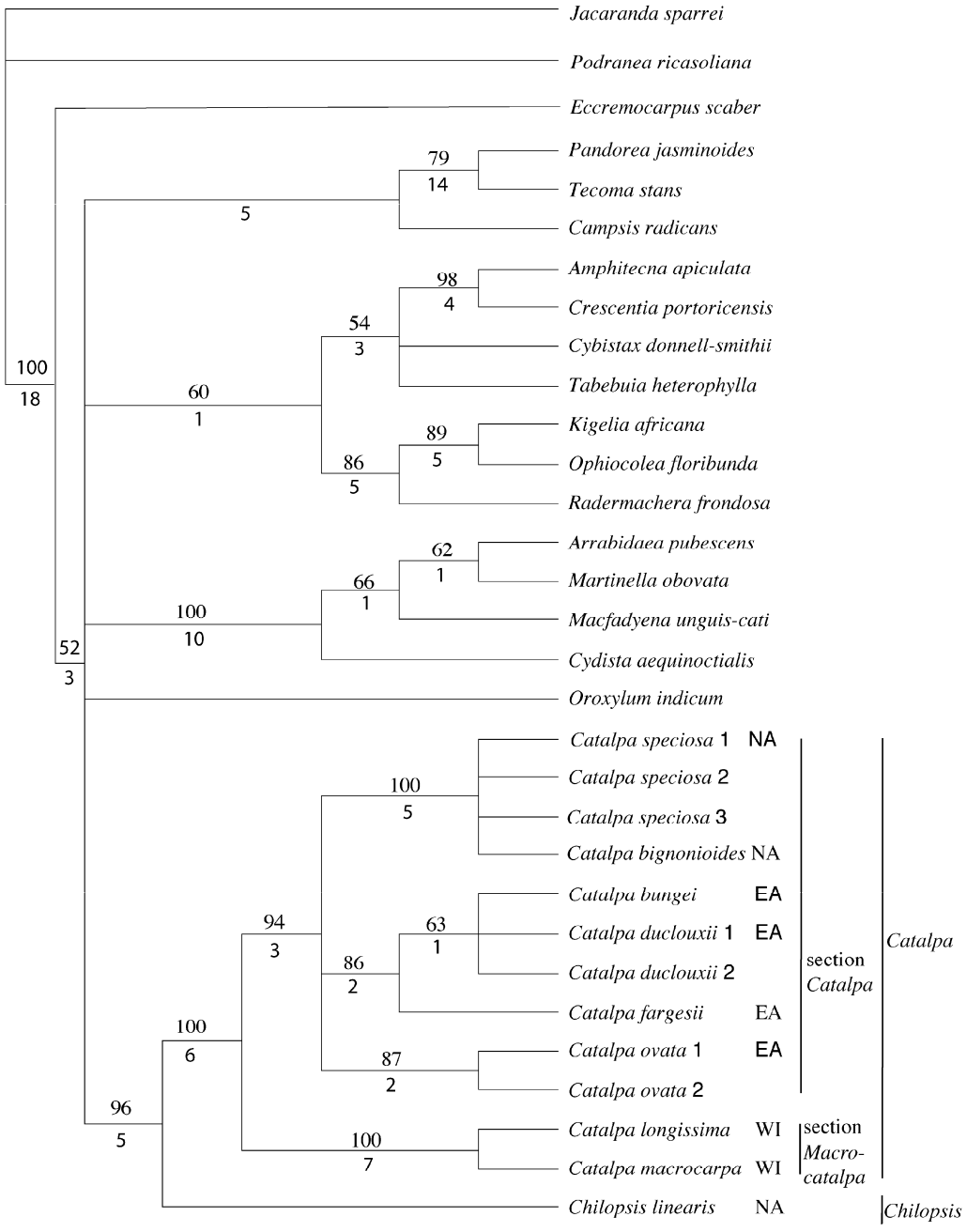

Fig. 1. Strict consensus of 14 parsimonious trees of 441 steps inferred from *ndhF* sequences. Numbers above branches are bootstrap support percentages. *CI*=0.82, *RI*=0.79. Numbers after species indicate accessions. EA, eastern Asia; NA, North America; WI, West Indies.

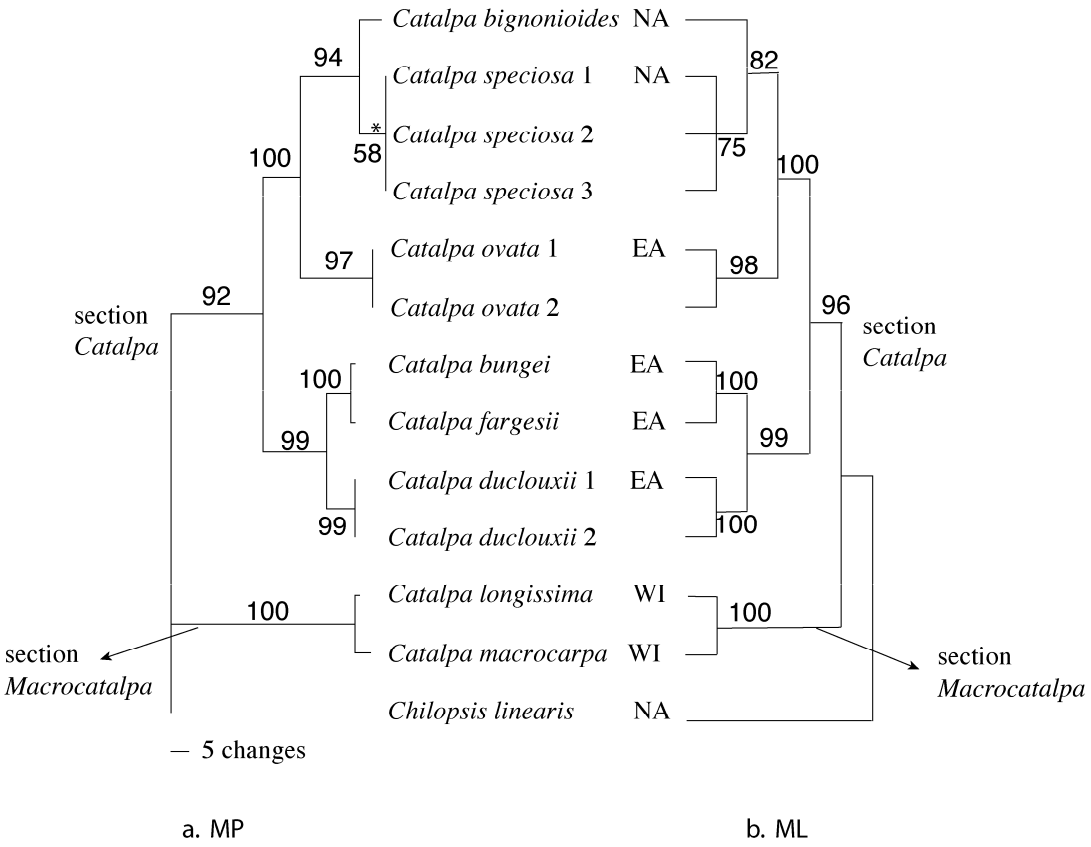

Fig. 2. nrDNA ITS trees. **a**, One of the 3 parsimonious trees of 117 steps (*CI*=0.88, *RI*=0.92). **b**, Single maximum likelihood tree (–ln=1513.9849). Numbers at branches are bootstrap percentages. Asterisk indicates that the clade is absent in the strict consensus tree. EA, eastern Asia; NA, North America; WI, West Indies.

share white flowers and other morphological characters (e.g., panicle inflorescence and greenish axillary buds). Natural hybrids have been found in the southeastern Missouri where the two species have overlapping distribution ranges (Brown, 1920). Nevertheless, *Catalpa speciosa* flowers in the mid-June in Boston, Massachusetts, while *C. bignonioides* blooms 10–15 days later (my personal observation). *Catalpa speciosa* has slightly fewer but larger flowers, fruits, and seeds compared with *C. bignonioides* (Garman, 1912). *Catalpa speciosa* and *C. bignonioides* are strongly supported as a clade, reflecting their close affinity (Figs. 1, 2).

Catalpa ovata, an eastern Asian species, is more closely related to eastern North American species, *C. speciosa* and *C. bignonioides*, than to other eastern Asian species (Fig. 2). Interestingly, fertile hybrids have been reported between *C. ovata* and either of the two eastern North American species. The hybrids grow faster and produce more seeds than either parent (Sargent, 1889; Jones & Filley, 1920; Smith & Nichols, 1941; Duffield & Snyder, 1958). All three species have leaves with five basal primary veins and large panicles (Paclt, 1952). Dode (1907) described *Catalpa duclouxii* based on specimens collected in Yunnan, China. This species differs from *C. fargesii* in the glabrous leaf undersurface and inflorescence, and the more branched inflorescence. Rehder (1913) treated *C. duclouxii* as a variety of *C. fargesii*. Gilmour (1936) further reduced *C. duclouxii* to a form of *C. fargesii*. These treatments imply that *C. duclouxii* is more closely related to *C. fargesii* than to *C. bungei*. In the ITS and combined trees (Fig. 2), *C. duclouxii* forms a clade that is sister to the clade containing *C. fargesii* and *C. bungei*. Therefore, our results do not support the close relationship of *C. duclouxii* and *C. fargesii*, as suggested by Rehder (1913) and Gilmour (1936).

The eastern Asian-eastern North American disjunction has attracted the attention of systematists and biogeographers since the nineteenth century (Gray, 1846, 1859; Chaney, 1947; Axelrod, 1960; Wolfe, 1975; Boufford & Spongberg, 1983; Wu, 1983; Tiffney, 1985a, b; Hong, 1993; Axelrod et al., 1998;

Guo, 1999; Manchester, 1999; Qian & Ricklefs, 1999; Wen, 1999; Donoghue et al., 2001; Stewart & Lister, 2001). Recent phylogenetic analyses of the disjunct plant genera, albeit limited in number, have provided valuable insights into pathways of migration and patterns of diversification of plant lineages around the Northern Hemisphere (Donoghue et al., 2001; Manos & Donoghue, 2001; Xiang & Soltis, 2001; Donoghue & Smith, 2004). However, in over 90 genera of the disjunct distribution between eastern Asia and North American disjunction, there are only six genera extending their distributions to the Caribbean islands. So far, none of them have been studied in a phylogenetic framework. In *Catalpa*, the WI species diverged from the continental species, while North American species may have come from Asia at a later time since they are embedded in an Asian clade (Fig. 2). It remains to be seen whether this is a general pattern in other EAS-NA disjunct genera (e.g., *Lyonia* and *Pieris*).

4 Conclusions

Sequences of the chloroplast *ndhF* gene support the sister relationship of *Chilopsis* and *Catalpa*, and within *Catalpa* the sequence data recognize sections *Macrocatalpa* and *Catalpa*. EAS species of section *Catalpa* do not form a clade. Instead, *Catalpa ovata* is more closely related to NA species than to other EAS species, which form a clade. The WI species diverged from EAS-NA continental species during the early evolutionary history of *Catalpa*. Phylogenetic studies of more disjunct genera with species in the WI are warranted to test whether the early separation of the WI species from continental lineages is a general pattern.

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