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Source: *International Journal of Plant Sciences*, Vol. 175, No. 6 (July/August 2014), pp. 613-650

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/676675>

Accessed: 02/11/2015 13:34

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ANGIOSPERM PHYLOGENY BASED ON 18S/26S rDNA SEQUENCE DATA: CONSTRUCTING A LARGE DATA SET USING NEXT-GENERATION SEQUENCE DATA

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Editor: Erika Edwards

The utility of 18S and 26S in broad phylogenetic analyses has been much maligned due in large part to the low signal in both genes. However, few analyses have employed complete 26S rDNA sequences over a broad range of taxa, and most alignments of the two genes are done *de novo*, without taking into account the secondary structure of the two rRNA genes. Here we mine next-generation sequence data to compile large matrices (429 taxa) of complete 18S + 26S gene sequences, and we compare both *de novo* alignment methods with curated alignments done by eye that take into account secondary structure and hard-to-align regions (profile alignments). The combined 18S + 26S topology is overall very similar to recently published gene trees for the angiosperms based on three or more genes. Overall support for the backbone or framework of the combined tree is low (bootstrap support below 50%). Few major clades have bootstrap support above 50%. Most well-supported clades are tip clades (families and orders *sensu* APG III 2009). Importantly, the 18S + 26S rDNA topology is consistent with current estimates of relationships: the basalmost angiosperms are recovered (*Amborellaceae*, *Nymphaeales*, *Austrobaileyales*), as are most major clades, including *Mesangiospermae*, eudicots (*Eudicotyledoneae* *sensu* Cantino et al. 2007), core eudicots (*Gunneridae* *sensu* Cantino et al. 2007), rosids (*Rosidae* *sensu* Cantino et al. 2007), asterids (*Asteridae* *sensu* Cantino et al. 2007), and *Caryophyllales*. Most clades recognized at the ordinal level (*sensu* APG III 2009) are also recovered. However, there are also some unusual placements in the 18S + 26S topology, but none of these receives bootstrap support above 50%. The profile and *de novo* alignments gave very similar topologies. 18S + 26S trees remain useful sources of data in large combined analyses. This is the first time a large data set of complete 26S gene sequences has been employed at this scale; this gene in particular proved to be useful phylogenetically. Targeted sequencing of 18S/26S rDNA is not advocated here, but given that these regions provide useful phylogenetic information and are abundant in next-generation sequencing runs, we suggest that the data be used rather than discarded.

Keywords: angiosperm tree of life, large data sets, next-generation sequencing, phylogenetics.

Online enhancements: appendix figures.

Introduction

Although much of what we now know about deep-level relationships in angiosperms relies on data from the plastid genome (reviewed in Soltis et al. 2005, 2011), the 18S and 26S nuclear ribosomal DNA regions were the early workhorses in plant molecular systematics (Hamby and Zimmer 1988, 1992; Nickrent and Franchina 1990; Nickrent and Starr 1994; Nickrent and Soltis 1995). These two regions, particularly the 18S rDNA, were major early tools for phylogenetic inference.

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Manuscript received April 2013; revised manuscript received February 2014; electronically published May 29, 2014.

The ease of amplification, conserved structure and evolution, and concerted evolution (this tandemly repeated region behaves as a “single-copy” gene) are all reasons for the early use of these regions not only in plant molecular phylogenetics but also in studies of diverse clades across much of life (reviewed in Soltis and Soltis 1998).

In plants, a series of studies explored the utility of 18S rDNA for phylogenetic inference (Hamby and Zimmer 1988, 1992; Nickrent and Franchina 1990; Nickrent and Soltis 1995; Kron 1996; Soltis et al. 1997). These studies provided important early insights into phylogenetic relationships. For example, 18S rDNA trees were the first to reveal the pivotal phylogenetic position of *Amborella* as one of the basalmost branches of the angiosperm tree of life (Soltis et al. 1997).



Table 1
Data Set Characteristics for Analyses

	18S	26S	18S + 26S combined
		Strict	Full
Families	393	258	242
Genera	1470	535	418
Species	1973	673	427
Total taxa	2264	732	429
Aligned bp de novo	2261	4028	5782
Aligned bp profile	2227	3916	6024
			6143

The utility of partial 26S rDNA sequences was also demonstrated in early studies (Hamby and Zimmer 1992; Bult and Zimmer 1993; Bult et al. 1995; Stefanovic et al. 1998). However, despite this potential, the phylogenetic utility of the entire 26S rDNA gene was questioned for several reasons, including the presence of large, potentially problematic expansion segments (reviewed in Kuzoff et al. 1998). In addition, because of the much longer length of the 26S rDNA region (~3400 bp, compared with ~1800 bp for the 18S rDNA), complete sequencing of the 26S rDNA lagged behind that of the 18S region. Kuzoff et al. (1998) ultimately demonstrated the utility of complete 26S rDNA sequence data in phylogeny reconstruction using a small set of angiosperms and also provided a suite of conserved primers with broad utility. However, given the length of 26S rDNA, two PCRs were typically required to obtain the entire 26S rDNA region. As a result, many investigators did not sequence the 26S rDNA in its entirety but rather employed only a portion of the gene.

Sequencing of 26S rDNA also provided important phylogenetic insights, typically when combined with other genes (Chanderbali et al. 2001; Neyland 2001; Simmons et al. 2001; Nickrent et al. 2002; Zanis et al. 2002; Fan and Xiang 2003). For example, 26S rDNA revealed that *Cuscuta* was derived within Convolvulaceae (Neyland 2001) and resolved relationships in Cornales (Fan and Xiang 2001). Sequences of 26S also helped resolve the basalmost angiosperm lineages (Zanis et al. 2002) and were among the first to reveal that Gunneraceae are sister to all other core eudicots (Soltis et al. 2003).

However, for both the 18S and 26S rDNA regions, rates of nucleotide substitution are generally low (Kuzoff et al. 1998; Soltis and Soltis 1998); hence, resolution and internal (bootstrap [BS]) support are low with these regions, even when combined with each other. As a result, more and more studies relied on increasingly large data sets of plastid genes (Givnish et al. 2010; Moore et al. 2010) and mitochondrial genes (Qiu et al. 2010) as well as combined data sets of plastid, mtDNA, and 18S/26S rDNA genes (Soltis et al. 2011). However, even in recent combined analyses, rDNA played an increasingly small role, often remaining unsequenced for large portions of the taxa. Although it is generally assumed that resolution and support with 18S + 26S data sets are very low, few studies have actually employed complete or nearly complete 26S

rDNA sequences. In contrast, nearly complete 18S rRNA gene sequences are numerous. Furthermore, taxonomic coverage of the angiosperms for 26S rDNA remains sparse—complete sequences for the 26S rDNA region are few compared with other genes. For example, the percentage of taxa in the final 17-gene, 640-taxon matrix for angiosperms that are represented by 26S rDNA sequences is only 57% (Soltis et al. 2011). Representation for 18S rDNA in the same matrix was much higher, at 78%. In contrast, plastid genes are much better represented. For example, 92% and 98% of all taxa are represented, respectively, for *matK* and *rbcL* in the 17-gene matrix.

Furthermore, secondary structure is an important feature of rDNA that needs to be considered in alignment of this region (Soltis and Soltis 1998). Whereas this was taken into consideration in early studies, with those regions carefully aligned by eye (Soltis et al. 1997, 2003), recent studies have gone back to the raw sequences from GenBank, and the sequences were then realigned using automated alignment programs without consideration of secondary structure.

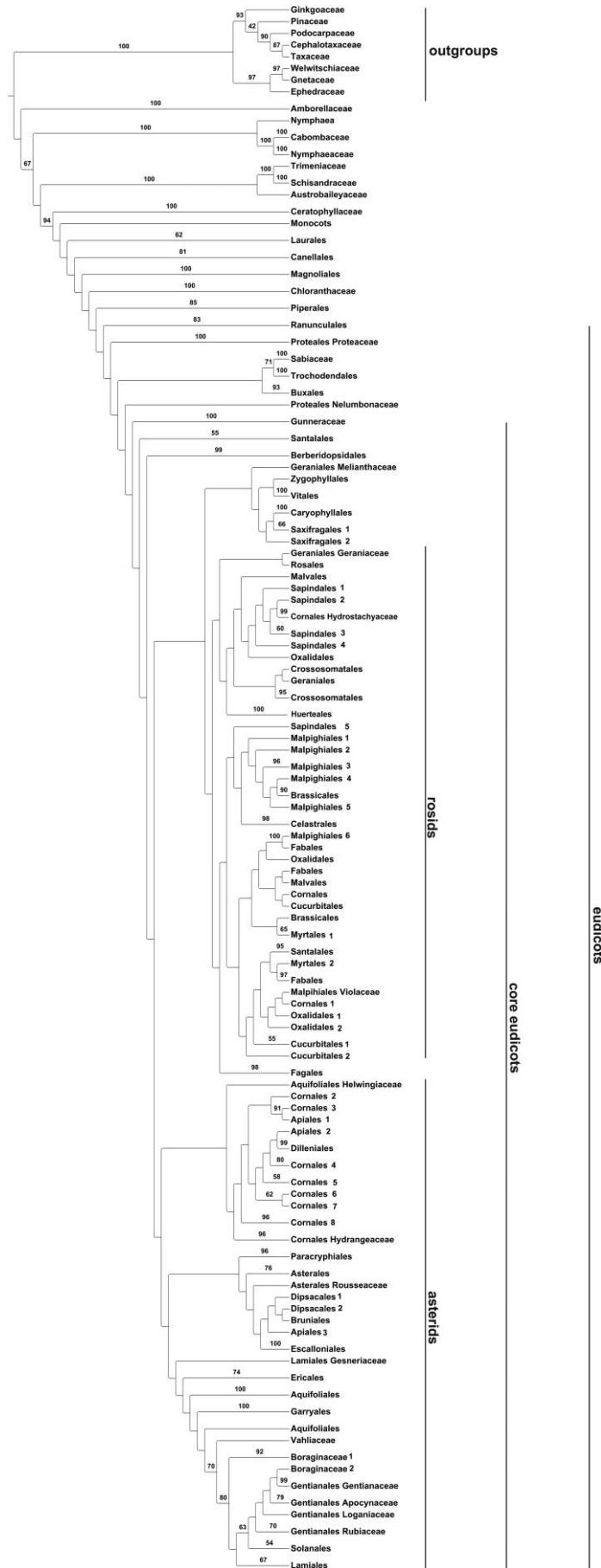
Sequences of 26S rDNA and 18S rDNA are routinely generated in abundance as a by-product of next-generation sequencing (NGS) efforts yet are standardly discarded on the basis of the now-widespread belief that they offer little to phylogenetic studies. Should these regions be used or ignored in future NGS efforts? Given the paucity of complete 26S rDNA sequences for angiosperms (and to a lesser extent 18S rDNA sequences), one goal was to assemble a large data set for these regions to reassess their utility at deep levels. Much of the data used here were obtained from GenBank, but especially for 26S rDNA data were mined from transcriptome data sets, highlighting rRNA sequences as a by-product of transcriptome studies even when steps have been taken to reduce rRNA presence. We also employed earlier alignments that incorporated knowledge of secondary structure with a second goal of assessing the impact of different alignment methods. We stress that our overarching goal here is not to promote targeted sequencing of 18S/26S rDNA but to evaluate anew the utility of these regions—if they provide useful phylogenetic information at deep levels and are abundant in NGS runs, why not use rather than discard the sequence data?

Material and Methods

Complete or nearly complete sequences for 18S and 26S rRNA genes were downloaded from GenBank, comprising 2256 and 501 accessions, respectively. Gymnosperm taxa were used as the outgroup. GenBank accession numbers are presented in appendix A.

We also used extensive NGS data (most from the 1000 Plant Transcriptome [1KP] Project; see below) to extract complete 18S and 26S rDNA sequences from numerous taxa. Since the number of angiosperm families represented by 18S rDNA sequences in GenBank is considerably larger than the number having complete (or even partial) 26S rDNA sequences (142 more families have 18S rDNA compared with 26S rDNA), our

Fig. 1 Summary tree of the best maximum likelihood 18S rDNA tree (de novo alignment), from the 18S complete data set. Numbers above branches are bootstrap values. In some cases clade names do not exactly match the composition of that clade sensu APG III (2009).



primary goal was to increase the number of families represented by the latter. We added 231 sequences for 26S rDNA and 75 sequences for 18S rDNA (app. B). In one set of analyses we assembled a data set in which all species are represented by both 18S and 26S rDNA sequences, resulting in a data set of 427 species (table 1; combined strict). We also constructed a second, much larger data set in which 26S rDNA was missing for some taxa; this data set had 2008 species and 2179 taxa (table 1; combined full).

Data Set Assembly

The 1KP Project (<http://www.onekp.com>) is a public-private partnership with the goal of sequencing 1000 plant transcriptomes. Samples span a broad phylogenetic range across all green plants, including representatives from chlorophyte algae through angiosperms. The sequencing goal of the 1KP Project is to generate ~2 Gbp of transcriptomic data using 100-bp paired-end Illumina sequencing. Johnson et al. (2012) outline the various sample preparation methods used for the project. At the time of this analysis, the 1KP Project was assembling these reads with the SOAPdenovo assembler (Li et al. 2010), and highly expressed genes like 18S and 26S were poorly represented in the final assemblies (V. H. Maia, M. A. Gitzen-danner, personal observation). Given the challenges of whole-transcriptome assembly and that we are interested in a very small subset of the data, we chose to pull reads from the raw read files that match 18S and 26S and assemble those independently.

To pull relevant reads from the raw sequence files, we used blat (ver. 34; Kent 2002) with a data set consisting of 18S and 26S rDNA sequences from Soltis et al. (2011) and the default options. If either read of a pair had a significant blat match, both reads were pulled into the set of selected reads. The set of selected reads was then assembled with Velvet (ver. 1.1; Zerbino and Birney 2008) using a kmer hash length of 55 and default options. The resulting contigs were imported into Geneious (ver. 5.4; <http://www.geneious.com>), and BLAST searches against the Soltis et al. (2011) data set were conducted to identify contigs with significant similarity (e -value $< 1.0e^{-1}$) to 18S and 26S sequences. As most assemblies resulted in multiple contigs per region (rather than a single contig for each region), the matching contigs were aligned to consensus 18S and 26S sequences to orient contigs along the genes (Geneious Alignment, default options). These contigs were then combined into a single 18S and a single 26S contig for each taxon, stitching contigs together with missing data characters as necessary.

Alignment

Sequence alignment was conducted on MAFFT (ver. 6.903; Katoh and Toh 2008) at the DNA level using the l-ins-i algorithm and default alignment parameters. We used two different alignment strategies: de novo alignment and profile alignment (--add option of MAFFT), in which the new alignment preserves the main structure of a given alignment, adding

the new sequences. For the profile alignments, the hand-curated alignments from Soltis et al. (2000) were used for 18S rDNA, and the alignment provided by Soltis et al. (2003) was employed for 26S rDNA; these were used as the profile alignment, and new sequences were added to these.

Phylogenetic Analysis

Phylogenetic analyses using maximum likelihood (ML; Felsenstein 1973) were conducted in the program RAxML (ver. 7.3.0; Stamatakis 2006). Model selection was conducted in JModelTest (Posada and Crandall 1998). Full analyses consisted of 100 BS replicates followed by a ML search, using the GTRGAMMA model as supported by JModelTest results. We conducted analyses on 18S and 26S rDNA data sets separately as well as on the combined rDNA data sets (profile and de novo). Data sets are described in table 1. The combined data set includes species with both 18S and 26S sequence data (strict combined analyses), totaling 429 taxa; in some cases we combined sequences for different species in the same genus (app. C). We also made combined analyses (profile and de novo) including complete 18S and 26S rDNA data sets (figs. D1, D2, available online). Alignments and phylogenetic trees were submitted to Dryad (doi:10.5061/dryad.bk827).

Results and Discussion

Separate 18S and 26S Trees

The best individual 18S rDNA tree (summarized in fig. 1; de novo alignment) is poorly resolved and supported; portions of the tree also have an unusual topology. For example, the monocot clade is not recovered. Instead, a grade of monocot lineages is sister to all remaining angiosperms; one subclade (Pandanales) is sister to all other angiosperms. Ceratophyllaceae are nested within monocot lineages (*Ceratophyllum* has appeared with monocots in some previous analyses; reviewed in Soltis et al. 2005). *Amborella* appears within a clade of Austrobaileyales, Nymphaeales, Piperales, and Proteales. The magnoliid clade (*Magnoliidae*) is not recovered. Nearly all eudicots, with the exception of Ranunculales, do form a clade. However, Ranunculales are recovered as sister to Austrobaileyales, Amborellaceae, Nymphaeales, Piperales, and Proteales, plus monocots. Within the eudicots, Gunnerales are sister to many asterids, and Caryophyllales are recovered (BS = 80%) within the asterids.

However, none of these unusual relationships above has BS support above 50%, and many aspects of the tree are in concordance with recent multigene analyses (Soltis et al. 2011). For example, the rosids largely form a clade. The asterids form a clade with Ericales and Cornales sister to the remaining members; lamiids and campanulids are largely intact.

The overall topology of the 26S rDNA tree (fig. 2; de novo alignment) resembles closely the tree of the combined 18S + 26S rDNA analysis. *Amborella* is sister to all other angiosperms, followed by Nymphaeales and Austrobaileyales; the

Fig. 2 Summary tree of the best maximum likelihood 26S rDNA tree (de novo alignment), from the 26S complete data set. Numbers above branches are bootstrap values. In some cases clade names do not exactly match the composition of that clade sensu APG III (2009).

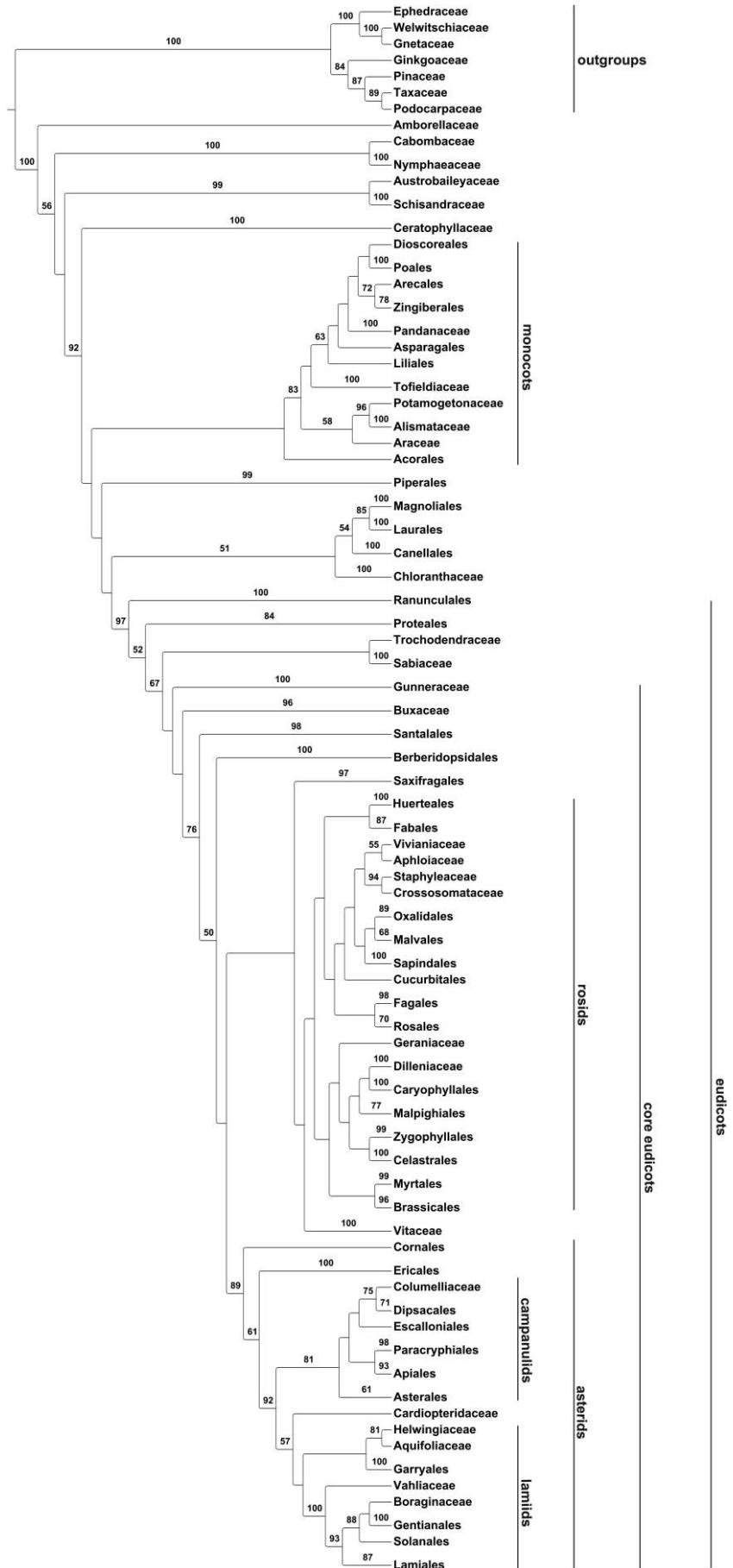


Table 2

Summary of Similarities and Conflicts between Topologies from Profile and De Novo 18S + 26S Data Sets

Major group	18S + 26S profile alignment	18S + 26S de novo alignment
Amborellaceae	Sister to Nymphaeales (BS = 55%)	Sister to (Nymphaeales + other angiosperms) (BS = 56%)
Asterids	Monophyletic (BS = 91%)	Monophyletic (BS = 89%)
Caryophyllales	Monophyletic within rosids (BS = 100%); sister to Zygophyllales	Monophyletic within rosids (BS = 100%); sister to Dilleniaceae
Ceratophyllaceae	Within monocots	(Amborellaceae + (Nymphaeales + (Austrobaileyales + (Ceratophyllaceae + other angiosperms))))
Core asterids	Monophyletic (BS = 78%)	Monophyletic (BS = 92%)
Core eudicots	Monophyletic (BS = 65%)	Monophyletic
Ericales	Monophyletic Ericales are embedded within Cornales, forming a clade sister to core asterids	Sister to core asterids (BS = 62%)
Eudicots	Monophyletic (BS = 100%)	Monophyletic (BS = 97%)
<i>Mesangiospermae</i>	Monophyletic (BS = 93%)	Monophyletic (BS = 92%)
Monocots	Monophyletic including Ceratophyllaceae (BS = 50%)	Monophyletic
Piperales	Sister to eudicots	Sister to ((remaining magnoliids + Chloranthaceae) + eudicots)
Rosids	Monophyletic	Monophyletic

Note. Only bootstrap support (BS) values above 50% are shown.

latter is sister to all other angiosperms (*Mesangiospermae*). Within the *Mesangiospermae*, Ceratophyllaceae are sister to the rest of the angiosperms (magnoliids, Chloranthales, and eudicots). The magnoliid clade is not recovered, but the four magnoliid orders are recovered, each with BS support above 50%; Laurales, Canellales, Magnoliales, Chloranthales, and Piperales form a grade sister to the eudicots.

Within the eudicots, Ranunculales are sister to the remainder of the clade. Proteales are not recovered as monophyletic. After Ranunculales, Proteaceae are sister to the remaining eudicots. Proteaceae are then followed by a clade of (Sabiaceae + (Trocchodendraceae + Buxaceae)); Nelumbonaceae (Proteales) are then immediate sister to the core eudicots.

Within the core eudicots, Gunneraceae are sister to the remaining eudicots, and the following clades are recovered: Berberidopsidales, Santalales, Caryophyllales, and asterids. Caryophyllales are highly supported (BS = 100%), although they are sister to Saxifragales and appear within a small clade that also includes the rosid orders Vitales, Zygophyllales, and Geraniales. The remaining rosids do form a clade, however. Many rosid orders (sensu APG III 2009) are not recovered (exceptions are Zygophyllales, Vitales, Rosales, Huerteales, Brassicales, and Fagales).

Although the asterid clade is recovered, it also includes Dilleniaceae. Most asterid orders are not recovered (exceptions are Ericales, Garryales, Paracryphiales, and Solanales).

18S + 26S Overview

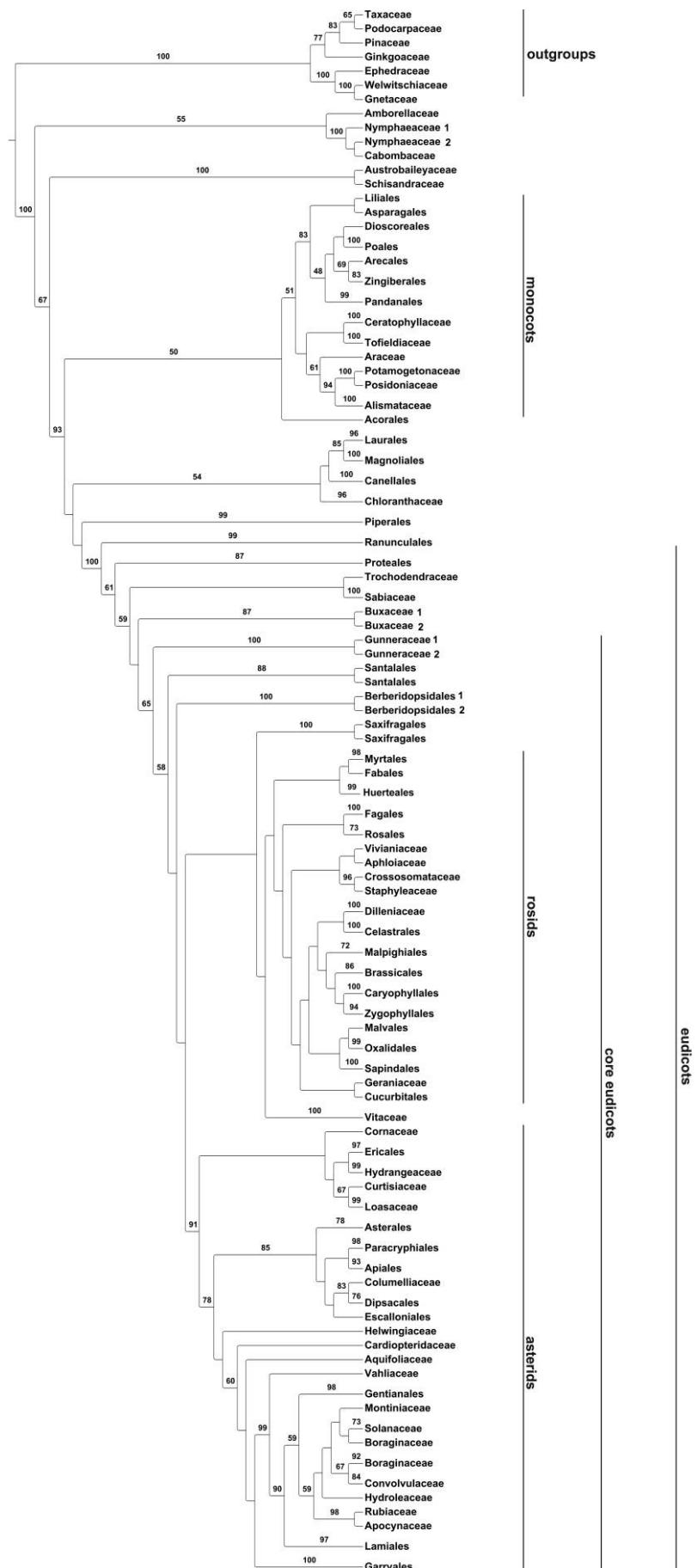
Significantly, the combined 18S + 26S topology (fig. 3; de novo alignment) is overall very similar to recently published gene trees for the angiosperms based on three or more genes (Soltis et al. 2000, 2011). Although the topology presented is

not meant to represent a dramatic improvement in our understanding of the framework of angiosperm phylogeny, this study does reveal that combined 18S + 26S gene sequences do a good job in recovering what we now believe is the angiosperm backbone tree. Certainly the overall internal support is low, which is not surprising given the low signal in these genes (reviewed in Kuzoff et al. 1998; Soltis et al. 1998, 1999, 2003). Thus, although 18S and 26S are often much maligned, these results do not support that claim. Most of our summary text of the topology is based on the profile alignment, which we describe in detail below. However, the two alignments gave very similar trees; the differences are summarized in a subsequent section of the article.

Overall support for most of the framework of the tree is low (BS < 50%). Few major clades have BS support above 50% (table 2). Most well-supported clades are tip clades (families and orders sensu APG III 2009). Importantly, most major clades are recovered with 18S + 26S, including *Mesangiospermae*, eudicots, core eudicots, rosids, asterids, and Caryophyllales. Most clades recognized at the ordinal level (sensu APG III 2009) are also recovered (table 2). However, there are some unusual placements in the 18S + 26S topology as well. None of these receives BS support above 50%, however. In fact, most of the overall 18S + 26S topology is not well supported, as has typified analyses in the past that have employed these genes. This overall low support is the result of the low signal present in these highly conserved regions (reviewed in Nickrent and Soltis 1995; Soltis and Soltis 1998; Soltis et al. 1999). We compare below in more detail the 18S + 26S topology we obtained here with the recent 17-gene tree for 640 angiosperms (Soltis et al. 2011).

Amborellaceae and Nymphaeaceae are either subsequent sis-

Fig. 3 Summary tree of the best maximum likelihood 18S + 26S rDNA tree (de novo alignment), from the strict combined 18S and 26S data sets. Numbers above branches are bootstrap values. In some cases clade names do not exactly match the composition of that clade sensu APG III (2009).



ters to all other angiosperms (*de novo* alignment) or form a clade that is sister to all other angiosperms (profile alignment; see below); both topologies have been found in other analyses (reviewed in Soltis et al. 2005, 2011). Amborellaceae and Nymphaeaceae are then followed by Austrobaileyales as subsequent sisters to all other angiosperms (*Mesangiospermae* sensu Cantino et al. 2007). Within the *Mesangiospermae*, monocots (*Monocotyledoneae*) are sister to the rest of the angiosperms (magnoliids, Chloranthales, and eudicots).

Within the monocots, Acoraceae, followed by Alismatales, are sister to the remaining monocots, as has been reported elsewhere (Chase et al. 2006; Soltis et al. 2011). However, a noteworthy difference in the 18S + 26S topology is that in this analysis Ceratophyllaceae appear within the monocots as part of Alismatales; in most multigene analyses, they appear either as sister to eudicots or, in some studies, as sister to monocots (reviewed in Soltis et al. 2005). Other clades of monocots recognized at the ordinal level in APG III (2009) are recovered, including Arecales, Asparagales, Liliales, Poales, and Zingiberales, although relationships among these clades are not necessarily congruent with other analyses of monocots (see Chase et al. 2006). In part, this could be due to the poor representation of monocots in the present study, as well as low signal (noted earlier). As in other analyses, Poales appear with Zingiberales and Asparagales with Liliales.

Following the monocots, the magnoliid clade is not recovered as monophyletic in this analysis of 18S + 26S. Instead, Chloranthales appear with most of the *Magnoliidae* clade as sister to (Laurales + Magnoliales) + Canellales (albeit without support above 50%). This Chloranthales + ((Laurales + Magnoliales) + Canellales) clade is in turn sister to Piperales (the fourth subclade that is typically part of *Magnoliidae*). Piperales are then the immediate sister to the eudicots (*Eudicotyledoneae*).

Within the eudicots, Ranunculales are sister to the remainder of the clade, as reported in other multigene analyses. Furthermore, the other basal eudicot clades are also recovered as subsequent sisters to the core eudicots (*Gunneridae*). That is, after Ranunculales, Proteales followed by Sabiaceae + Trochodendraceae and then Buxaceae are sister to the core eudicots. These same clades have been consistently recovered as subsequent sisters to the core eudicots in multigene analyses, although the branching order and relationships among them frequently differ from study to study, with BS support often low. With 17 genes, Proteales + Sabiaceae (BS = 59%) are sister to Trochodendraceae, followed by Buxaceae as sisters to core eudicots.

Within Ranunculales, relationships also closely follow those recovered with many more genes, with Eupteleaceae followed by Papaveraceae sister to the remainder, which comprise two subclades: (1) Lardizabalaceae + Circaeasteraceae and (2) Menispermaceae sister to Ranunculaceae + Berberidaceae.

Within the core eudicots, Gunneraceae are sister to the remaining eudicots (*Pentapetalae* sensu Cantino et al. 2007), a relationship that has been consistently recovered with three or

more genes. Within the core eudicots, all of the major (and minor) subclades found in multigene analyses are recovered here: Berberidopsidales, Santalales, Caryophyllales, Saxifragales, and asterids (*Asteridae*). However, Caryophyllales are embedded within the large rosid clade. We found that the placement of Caryophyllales varied from analysis to analysis in our study.

Within the *Pentapetalae*, Santalales followed by Berberidopsidales are sister to two large clades: (1) Saxifragales sister to Vitaceae + rosids (including Caryophyllales) and (2) asterids. Relationships among these major subclades of *Pentapetalae* have been very difficult to resolve—only in studies employing 17 genes (Soltis et al. 2011) and most of the chloroplast genome or inverted repeat (Moore et al. 2010, 2011) were relationships resolved. Hence, 18S + 26S alone did surprisingly well, with the exception of the placement of Caryophyllales.

Our analyses recovered Saxifragales as sister to Vitaceae + rosids, a result also recovered with numerous genes, with the caveat that Caryophyllales are embedded within the rosids. Within Saxifragales, relationships largely mirror multigene analyses: there is a clade of woody families (e.g., Hamamelidaceae, Altingiaceae, and Cercidiphyllaceae) sister to a core group of families that includes Iteaceae, Grossulariaceae, Saxifragaceae, and Crassulaceae. Paeoniaceae are sister to this latter clade, whereas in studies involving numerous genes Paeoniaceae are sister to the woody families—but this is a relationship that was very difficult to resolve.

Within the rosids, many of the clades recognized at the ordinal level are again recovered. However, broader relationships within the rosid clade showed some similarities to multigene analyses as well as some striking differences. Particularly problematic is the placement of Caryophyllales as immediate sister to Zyophyllales; this clade is in turn sister to Brassicales. The two large subclades of rosids (malvids and fabids) are not recovered here. The nitrogen-fixing clade (Soltis et al. 1995) was also not recovered with 18S + 26S sequence data.

Within the Caryophyllales, relationships largely mirror those achieved with many genes (Brockington et al. 2009). Two major subclades are recovered. A clade of Polygonaceae, Tamaricaceae, Dioncophyllaceae, Droseraceae, and Nepenthaceae is sister to the remaining families. Considering the second major subclade, Rhabdodendraceae followed by Asteropeiaceae + Physenaceae are sister to the remainder (Simmondsiaceae were not included).

Within the asterid clade, most clades recognized as orders in APG III (2009) are recovered. Overall relationships within the asterids closely mirror those obtained with numerous genes, with a few exceptions. Cornales + Ericales are sister to the core asterids, rather than Cornales followed by Ericales sister to core asterids (see Soltis et al. 2011). The core asterids comprise two large subclades: lamiids and campanulids.

An unusual feature of the asterid portion of the topology is that a mixture of Garryales plus Aquifoliales appear as a grade

Fig. 4 Summary of the best maximum likelihood 18S + 26S rDNA tree (profile alignment), from the strict combined 18S and 26S data sets. Numbers above branches are bootstrap values. In some cases clade names do not exactly match the composition of that clade sensu APG III (2009).

to the remainder of the lamiid clade. In multigene topologies, Aquifoliales are sister to remaining campanulids, and Garryales are sister to the remaining lamiids (Soltis et al. 2011). As with other unusual relationships recovered with 18S + 26S, there is not BS support above 50% for this result.

Relationships within the campanulid clade have been well studied by Tank and Donoghue (2010). Within the campanulid clade, 18S + 26S recover Escalloniales + (Dipsacales + Columelliaceae) plus (Apiales + Paracryphiales) as sister to Asterales. In contrast, in Tank and Donoghue (2010) Escalloniales are sister to ((Bruniaceae + Columelliaceae) + Apiales + (Paracryphiales + Dipsacales)), but in the 18S + 26S tree only Columelliaceae + Dipsacales receives support above 50%. The composition and relationships within Asterales are a close match to those recovered with 17 genes and in Tank and Donoghue (2010). For example, Menyanthaceae, Goodeniaceae, and Calyceraceae are recovered as successive sisters to Asteraceae.

There are also differences between the 18S + 26S trees obtained here compared with recent analyses of lamiids, although none well supported. Within lamiids, Garryales do not appear as sister to the remainder of the clade. Helwingiaceae, Cardiopteridaceae (placed in Aquifoliales), the rest of Aquifoliales, and then Garryales appear as subsequent sister groups to the remaining lamiids. Vahliaceae are sister to the remainder of lamiids, as is the case with 17 genes. Boraginaceae plus Solanales are sister to Gentianales—this clade is in turn sister to Lamiales with the de novo alignment (with the profile alignment, Boraginaceae are not monophyletic). With 17 genes, Boraginaceae are instead sister to Lamiales, but again without support above 50%; the placement of this family remains enigmatic. Relationships within subclades of lamiids, such as Lamiales, are poorly resolved. We stress, however, that relationships within Lamiales in particular have been hard to resolve even with numerous genes, apparently as a result of rapid radiation (Schäferhoff et al. 2010; Soltis et al. 2011). Hence, despite differences, the overall topology for most of the lamiid clade, as well as the asterids in general, is actually very close to what is largely accepted on the basis of much larger compilations of genes.

Comparison of De Novo and Profile Alignments

We had hypothesized that the profile alignment would provide a better estimate of phylogeny than the de novo alignment in that the former would take into account the complex secondary structure of portions of the 18S and 26S rRNA regions (see Kuzoff et al. 1998; Soltis et al. 1998, 1999). However, phylogenetic analysis of the profile and the de novo alignments for 18S and 26S rDNA give very similar results. Examination of the de novo alignment and difficult-to-align regions of 18S rDNA revealed alignments that were generally very good. Alignment of these regions might have been improved by additional adjustments by eye, but only to a minor extent—it would certainly not be worth the additional effort. Similarly, while we did not make a major effort to delineate and examine all of the 26S expansion segments, the 26S rDNA de novo alignment also did not look problematic; researchers are unlikely to encounter problems with these segments.

The summary topologies of the 18S + 26S de novo and

profile alignments are provided in figures 3 and 4; the complete 18S + 26S de novo and profile alignment trees are given in figures D1 and D2. The main similarities and conflicts between these topologies are summarized in table 2. The most noteworthy differences between the trees generated via the two alignments include the following: (1) analysis of the de novo alignment places *Amborella* followed by Nymphaeales as subsequent sisters to all other flowering plants, whereas the profile alignment places a clade of *Amborella* + Nymphaeales as sister to all other angiosperms; (2) analysis of the profile alignment places Ceratophyllaceae with monocots, whereas the topology generated from the de novo alignment places Ceratophyllaceae after Amborellaceae, Nymphaeales, and Austrobaileyales as sister to all other angiosperms; (3) Piperales are sister to eudicots in the topology resulting from the profile alignment, but in the trees resulting from the de novo alignment they are sister to the remaining magnoliids + Chloranthaceae plus eudicots; (4) in the trees generated from the de novo alignment, Cornales followed by Ericales are sister to core asterids, which is the case in most recent analyses; however, in the topology obtained from the profile alignment a monophyletic Ericales are embedded within Cornales, and this clade is then sister to core asterids; and (5) Caryophyllales are sister to Dilleniaceae in the phylogenetic analysis of the de novo alignment and sister to Zygophyllales in the trees resulting from analysis of the profile alignment, but in phylogenetic analyses of both alignments, Caryophyllales as well as Dilleniaceae are embedded within the rosid clade. We stress, however, that none of these differences between the topologies generated from the profile and de novo alignments is well supported (BS < 50% for all).

As reviewed, both the 18S and 26S rDNA regions comprise large areas that are highly conserved not only across angiosperms but also across green life; these hyperconserved areas are interspersed with more variable regions. These largely correspond to stems and loops, respectively (Kuzoff et al. 1998; Soltis et al. 1998). The large data sets compiled here do not alter this overall picture of these regions. In addition, there are several possible explanations for the similar performance of de novo versus profile alignments. Initial comparisons of de novo versus profile alignments were conducted nearly 15 years ago and involved either alignment by eye or the alignment programs of that time period (e.g., CLUSTAL). Current alignment programs, such as those used here (MAFFT), may simply provide a much better de novo alignment than those used in comparisons between alignments that included knowledge of secondary structure and those that did not (Soltis et al. 1998). Alternatively, much of the signal at deeper levels is not in the harder-to-align regions (loops) but in stem regions, which are much easier to align. Soltis et al. (1998) provided some evidence for this hypothesis for 18S rDNA.

It has been possible to target the 18S and 26S rDNA regions (the variable as well as the more conserved areas) for some time now using widely available PCR primers (Kuzoff et al. 1998; Soltis et al. 1998, 2003). However, with the ease of NGS approaches, it is now easy to recover and align the entire regions as a by-product of other analyses. Our goal is not to promote targeted sequencing of 18S/26S regions—that is not worth the effort at this point given the ease of NGS approaches. We simply stress that rather than discarding 18S/26S sequence data (and potential information) following NGS, it is relatively

easy to employ sequences of these entire regions in phylogenetic analysis. Furthermore, the data are informative.

Summary

Although 18S and 26S rDNA sequence data have been much maligned, the large combined 18S + 26S rDNA topology we recovered is very similar to recently published gene trees for the angiosperms based on three or more genes. Overall support for most of the angiosperm framework is low (BS < 50%) in the combined 18S + 26S rDNA tree; few major clades have BS support above 50%. This low support is not surprising, however, given the low signal present in 18S and 26S rDNA. Importantly, with 18S + 26S rDNA sequence data the overall topology is consistent with most current estimates of relationships: the basalmost angiosperms are recovered (Amborellaceae, Nymphaeales, and Austrobaileyales), as are most major clades, including *Mesangiospermae*, eudicots, core eudicots, rosids, asterids, and Caryophyllales. In addition, most clades recognized at the ordinal level (sensu APG III 2009) are also recovered. There is no strongly supported conflict between 18S and 26S trees and those from other DNA regions. Thus, a large combined data set of complete (or nearly so) 18S + 26S rDNA sequences yields a very reasonable, albeit poorly supported, overall picture of angiosperm phylogeny. In summary, targeted sequencing of 18S/26S rDNA is not advocated here in this age of NGS. However, given that these regions provide

useful phylogenetic information and are abundant in NGS runs, we suggest the data be used rather than simply discarded.

Acknowledgments

We are grateful to the 1KP Project for the use of 18S and 26S rDNA sequence data, and in particular we thank the various collectors who made samples available for that project, including Mark Chase, Sean Graham, Jim Leebens-Mack, and Dennis Stevenson. The 1KP Consortium is supported by the government of Alberta (Ministry of Advanced Education and Technology), Musea Ventures, BGI-Shenzhen, Alberta's Informatics Circle of Research Excellence (iCORE), and iPlant (National Science Foundation grant DBI-0735191). The funds from Musea Ventures came in the form of a charitable donation to the University of Alberta. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank University of Florida Research Computing (<http://researchcomputing.ufl.edu>) for providing computational resources and support that have contributed to the research results reported in this publication. V. H. Maia was supported by Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). We also thank the reviewers for very helpful comments on the manuscript.

Appendix A

Sequences Downloaded from GenBank

The list is formatted as follows: gene, family, binomial name, GI number.

18S: Acanthaceae: *Pachystachys lutea*, gi17028060. Acanthaceae: *Avicennia marina*, gi34014987. Acanthaceae: *Acanthus ebracteatus*, gi34014988. Acanthaceae: *Barleria prionitis*, gi4558878. Acanthaceae: *Justicia americana*, gi4558879. Acanthaceae: *Thunbergia alata*, gi4558880. Acanthaceae: *Avicennia marina*, gi5514638. Aceraceae: *Acer rubrum*, gi1777632. Achariaceae: *Dasylepis brevipedicellata*, gi118918028. Achariaceae: *Campstostylus manni*, gi119368133. Achariaceae: *Ceratiosicyos laevis*, gi119368134. Achariaceae: *Kiggelaria africana*, gi119368135. Achariaceae: *Erythrospermum phytolaccoides*, gi261873435. Achariaceae: *Kiggelaria* sp., gi51320380. Achariaceae: *Acharia tragodes*, gi7595357. Achariaceae: *Kiggelaria africana*, gi7595465. Achariaceae: *Pangium edule*, gi7595499. Acoraceae: *Acorus calamus*, gi532564. Acoraceae: *Acorus gramineus*, gi6467914. Actinidiaceae: *Actinidia* sp., gi1777633. Actinidiaceae: *Actinidia chinensis*, gi33312021. Adoxaceae: *Sambucus canadensis*, gi11066013. Adoxaceae: *Adoxa moschatellina*, gi305671581. Adoxaceae: *Sambucus ebulus*, gi6689227. Adoxaceae: *Viburnum acerifolium*, gi6689555. Aextoxicaceae: *Aextoxicum punctatum*, gi7595359. Aizoaceae: *Tetragonia tetragonoides*, gi1777649. Aizoaceae: *Delosperma echinatum*, gi7595419. Alismataceae: *Sagittaria trifolia*, gi2346996. Alismataceae: *Ranalisma rostratum*, gi61741971. Alismataceae: *Limnocharis flava*, gi61741978. Alismataceae: *Hydrocleys nymphoides*, gi61741980. Alismataceae: *Caldesia oligococca*, gi61741988. Alismataceae: *Alisma plantago-aquatica*, gi6467915. Alseuosmiaceae: *Alseuosmia macrophylla*, gi7595364. Alstroemeriaceae: *Bomarea hirtella*, gi7595391. Altingiaceae: *Altingia* sp., gi1777674. Altingiaceae: *Liquidambar styraciflua*, gi1777684. Alzateaceae: *Alzatea verticillata*, gi133918016. Amaranthaceae: *Beta vulgaris*, gi261873471. Amaranthaceae: *Spinacia oleracea*, gi532649. Amaranthaceae: *Celosia argentea*, gi7595403. Amaryllidaceae: *Ipheion uniflorum*, gi312436248. Amaryllidaceae: *Agapanthus africanus*, gi313756773. Amaryllidaceae: *Lycoris uydensis*, gi313756774. Amaryllidaceae: *Allium thunbergii*, gi6273785. Amaryllidaceae: *Hippeastrum* sp., gi6273811. Amaryllidaceae: *Clivia nobilis*, gi7595409. Amborellaceae: *Amborella trichopoda*, gi1777635. Amphorogynaceae: *Dendrotrophe varians*, gi1008727. Amphorogynaceae: *Spirogardnera rubescens*, gi149930360. Amphorogynaceae: *Leptomeria spinosa*, gi149930362. Amphorogynaceae: *Choretrum glomeratum*, gi149930363. Amphorogynaceae: *Daenikera corallina*, gi149930364. Amphorogynaceae: *Choretrum pauciflorum*, gi156454151. Amphorogynaceae: *Dufrenoya sphaerocarpa*, gi2746746. Anacardiaceae: *Anacardium occidentale*, gi21070426. Anacardiaceae: *Mangifera indica*, gi289469965. Anacardiaceae: *Rhus taitensis*, gi290782502. Anacardiaceae: *Rhus typhina*, gi290782503. Anacardiaceae: *Searsia quartiniana*, gi290782504. Anacardiaceae: *Schinus molle*, gi7595535. Ancistrocladaceae: *Ancistrocladus korupensis*, gi7595366. Anisophylleaceae: *Anisophyllea fallax*, gi33330855. Anisophylleaceae: *Anisophyllea corneri*, gi66276220. Anisophylleaceae: *Combretocarpus rotundatus*, gi66276223. Annonaceae: *Polyalthia suberosa*, gi11066010. Annonaceae: *Isolona* sp., gi20514969. Annonaceae: *Cananga odorata*, gi22001094.

Annonaceae: *Annona muricata*, gi7595370. Annonaceae: *Asimina triloba*, gi7595376. Aphanopetalaceae: *Aphanopetalum resinosum*, gi9502206. Aphloiaceae: *Aphloia theiformis*, gi7595371. Apiaceae: *Lomatium triternatum*, gi1777646. Apiaceae: *Angelica gigas*, gi200116396. Apiaceae: *Cnidium officinale*, gi2645176. Apiaceae: *Ligusticum sinense*, gi2645177. Apiaceae: *Azorella caespitosa*, gi305671582. Apiaceae: *Mackinlaya confusa*, gi305671589. Apiaceae: *Apium graveolens*, gi7595372. Apiaceae: *Cnidium monnierii*, gi7707625. Apocynaceae: *Thevetia* sp., gi1777650. Apocynaceae: *Asclepias syriaca*, gi330441209. Apocynaceae: *Cerbera manghas*, gi34014991. Apocynaceae: *Alstonia scholaris*, gi4558881. Apocynaceae: *Apocynum* sp., gi4558882. Apocynaceae: *Nerium oleander*, gi4558883. Apodanthaceae: *Pilosyles berteroii*, gi301078582. Aponogetonaceae: *Aponogeton crispus*, gi6273786. Aquifoliaceae: *Ilex opaca*, gi6651251. Aquifoliaceae: *Ilex opaca*, gi7595458. 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Menispermaceae: *Menispermum canadense*, gi22595030. Menispermaceae: *Tinospora caffra*, gi22595031. Menispermaceae: *Cocculus trilobus*, gi66969205. Menyanthaceae: *Menyanthes trifoliata*, gi19919626. Menyanthaceae: *Nymphoides geminata*, gi19919627. Menyanthaceae: *Menyanthes trifoliata*, gi305671609. Molluginaceae: *Mollugo verticillata*, gi19919529. Monimiaceae: *Peumus boldus*, gi30527329. Montiniaceae: *Montinia caryophyllacea*, gi19919616. Moraceae: *Morus nigra*, gi19919673. Moraceae: *Maclura tricuspidata*, gi336239103. Moraceae: *Ficus tikoua*, gi336239108. Musaceae: *Musa acuminata*, gi169135229. Musaceae: *Musa acuminata*, gi169135230. Myodocarpaceae: *Delarbrea michieana*, gi19919637. Myodocarpaceae: *Delarbrea collina*, gi37778851. Myodocarpaceae: *Myodocarpus involucratus*, gi37778887. Myodocarpaceae: *Pseudosciadium balansae*, gi37778896. Myricaceae: *Morella cerifera*, gi19919688. Myristicaceae: *Mauloutchia chapelieri*, gi66969226. Myrothamnaceae: *Myrothamnus flabellifolia*, gi19919664. Myrtaceae: *Myrtus communis*, gi157689142. Nelumbonaceae: *Nelumbo lutea*, gi22595032. Nepenthaceae: *Nepenthes* sp., gi22595033. Neuradaceae: *Neurada procumbens*, gi19919666. Nitrariaceae: *Nitraria retusa*, gi157689143. Nymphaeaceae: *Nuphar* sp., gi110757092. Nymphaeaceae: *Nymphaea* sp., gi30527328. Ochnaceae: *Sauvagesia erecta*, gi133900046. Ochnaceae: *Medusagyne oppositifolia*, gi19919561. Oleaceae: *Olea europaea*, gi19919612. Onagraceae: *Clarkia xantiana*, gi19919589. Opiliaceae: *Opilia amentacea*, gi19919536. Orchidaceae: *Vanilla imperialis*, gi219964407. Oxalidaceae: *Averrhoa carambola*, gi19919568. Oxalidaceae: *Oxalis dillenii*, gi19919671. Papaveraceae: *Pteridophyllum racemosum*, gi19919661. Papaveraceae: *Dicentra eximia*, gi22595035. Papaveraceae: *Hypecoum imberbe*, gi22595036. Papaveraceae: *Pteridophyllum racemosum*, gi22595037. Papaveraceae: *Sanguinaria canadensis*, gi66969209. Paracryphiaceae: *Paracryphia alticola*, gi305671610. Paracryphiaceae: *Quintinia quatrefagesii*, gi305671611. Passifloraceae: *Passiflora edmundoi*, gi74272774. Paulowniaceae: *Paulownia tomentosa*, gi325071863. Peraceae: *Clutia pulchella*, gi133900035. Peraceae: *Pera bicolor*, gi133900041. Peraceae: *Pogonophora schomburgkiana*, gi133900042. Phellinaceae: *Phelline comosa*, gi19919629. Phyllanthaceae: *Bischofia javanica*, gi133900034. Phyllanthaceae: *Phyllanthus calycinus*, gi157689144. Phytolaccaceae: *Phytolacca dioica*, gi19919530. Picrodendraceae: *Androstachys johnsonii*, gi19919564. Pinaceae: *Pinus massoniana*, gi170515999. Piperaceae: *Peperomia obtusifolia*, gi110757089. Piperaceae: *Piper betle*, gi30527330. Pittosporaceae: *Pittosporum fairchildii*, gi19919633. Pittosporaceae: *Hymenosporum flavum*, gi37778871. Pittosporaceae: *Marianthus ringens*, gi37778876. Pittosporaceae: *Rhytidosporum alpinum*, gi37778898. Pittosporaceae: *Billardiera heterophylla*, gi37778901. Pittosporaceae: *Pittosporum tobira*, gi37778912. Plantaginaceae: *Veronica anagallis-aquatica*, gi19919610. Poaceae: *Capeochloa arundinacea*, gi167594336. Podocarpaceae: *Podocarpus macrophyllus*, gi66969252. Polemoniaceae: *Gilia capitata*, gi19919596. Polygalaceae: *Polygala cruciata*, gi19919674. Polygonaceae: *Fallopia sachalinensis*, gi19919526. Portulacaceae: *Portulaca grandiflora*, gi19919534. Potamogetonaceae: *Potamogeton berchtoldii*, gi66969237. Primulaceae: *Anagallis tenella*,

gi19919590. Primulaceae: *Androsace spinulifera*, gi19919591. Primulaceae: *Maesa myrsinoides*, gi19919593. Proteaceae: *Persoonia katerae*, gi110757085. Proteaceae: *Lambertia inermis*, gi19919647. Proteaceae: *Roupala macrophylla*, gi22595038. Rafflesiaceae: *Rhizanthes zippelii*, gi133900044. Ranunculaceae: *Coptis trifolia*, gi22595039. Ranunculaceae: *Glaucidium palmatum*, gi22595040. Ranunculaceae: *Hydrastis canadensis*, gi22595041. Ranunculaceae: *Ranunculus keniensis*, gi22595042. Ranunculaceae: *Xanthorhiza simplicissima*, gi22595043. Ranunculaceae: *Xanthorhiza simplicissima*, gi66969203. Rhabdodendraceae: *Rhabdodendron amazonicum*, gi19919528. Rhamnaceae: *Ceanothus sanguineus*, gi19919543. Rhamnaceae: *Gouania mauritiana*, gi336239110. Rhamnaceae: *Rhamnus utilis*, gi336239115. Rosaceae: *Spiraea betulifolia*, gi19919544. Rosaceae: *Dryas octopetala*, gi336239106. Rosaceae: *Filipendula vulgaris*, gi336239109. Rosaceae: *Sanguisorba sitchensis*, gi336239116. Rousseaceae: *Rousseea simplex*, gi19919684. Rubiaceae: *Coprosma montana*, gi284159163. Rutaceae: *Ruta graveolens*, gi32815122. Sabiaceae: *Meliosma veitchiorum*, gi22595044. Sabiaceae: *Sabia swinhoei*, gi22595045. Sabiaceae: *Meliosma squamulata*, gi66969197. Salicaceae: *Idesia polycarpa*, gi19919558. Salicaceae: *Populus tremuloides*, gi19919559. Santalaceae: *Osyris wightiana*, gi222476886. Santalaceae: *Eubrachion ambiguum*, gi22595046. Santalaceae: *Osyris lanceolata*, gi22595047. Santalaceae: *Santalum album*, gi63253807. Sapindaceae: *Cupaniopsis anacardioides*, gi19919580. Sarraceniaceae: *Sarracenia purpurea*, gi22595049. Sarraceniaceae: *Sarracenia purpurea*, gi30230613. Saururaceae: *Saururus cernuus*, gi30527331. Saururaceae: *Houttuynia cordata*, gi66969228. Saxifragaceae: *Heuchera micrantha*, gi19919652. Saxifragaceae: *Sullivantia oregana*, gi19919653. Saxifragaceae: *Saxifraga mertensiana*, gi19919665. Saxifragaceae: *Fendlera rupicola*, gi30230610. Schisandraceae: *Illicium verum*, gi170516057. Schisandraceae: *Kadsura japonica*, gi66969245. Schisandraceae: *Schisandra sphenanthera*, gi66969246. Schoepfiaceae: *Schoepfia schreberi*, gi22595034. Scrophulariaceae: *Myoporum mauritianum*, gi19919611. Siparunaceae: *Siparuna decipiens*, gi66969219. Solanaceae: *Nicotiana tabacum*, gi19919613. Solanaceae: *Schizanthus pinnatus*, gi19919614. Solanaceae: *Petunia axillaris*, gi19919615. Staphyleaceae: *Staphylea trifolia*, gi19919574. Stemonaceae: *Croomia pauciflora*, gi66969235. Stemonuraceae: *Irvingbaileya* sp., gi19919643. Strombosiaceae: *Diogoa zenkeri*, gi112408986. Stylidiaceae: *Donatia* sp., gi19919630. Styracaceae: *Styrax japonicus*, gi19919597. Styracaceae: *Halesia diptera*, gi19919598. Tamaricaceae: *Tamarix pentandra*, gi19919524. Tapisciaceae: *Tapiscia sinensis*, gi19919587. Taxaceae: *Taxus baccata*, gi170516191. Tetramelaceae: *Tetrameles nudiflora*, gi66276252. Tetrameristaceae: *Tetramerista* sp., gi19919594. Thymelaeaceae: *Thymelaea hirsuta*, gi19919675. Tofieldiaceae: *Pleea tenuifolia*, gi30527335. Tofieldiaceae: *Tofieldia calyculata*, gi66969241. Torricelliaceae: *Melanophylla alnifolia*, gi37778877. Torricelliaceae: *Torricellia tiliifolia*, gi37778905. Trimeniaceae: *Trimenia moorei*, gi30527333. Trochodendraceae: *Trochodendron aralioides*, gi19919646. Tropaeolaceae: *Tropaeolum tricolor*, gi19919585. Ulmaceae: *Celtis yunnanensis*, gi19919539. Ulmaceae: *Zelkova serrata*, gi19919540. Ulmaceae: *Celtis tetrandra*, gi336239102. Ulmaceae: *Ulmus macrocarpa*, gi336239118. Urticaceae: *Debregeasia saeneb*, gi336239104. Urticaceae: *Pilea cadierei*, gi336239114. Vahliaeae: *Vahlia capensis*, gi19919623. Verbenaceae: *Verbena scabridoglandulosa*, gi19919608. Violaceae: *Rinorea pubiflora*, gi62902797. Viscaceae: *Viscum album*, gi22595048. Vitaceae: *Vitis aestivalis*, gi19919648. Vivianiaceae: *Viviania marifolia*, gi19919571. Welwitschiaceae: *Welwitschia mirabilis*, gi110757094. Winteraceae: *Tasmannia insipida*, gi30527332. Winteraceae: *Takhtajania perrieri*, gi66969233. Xanthorrhoeaceae: *Bulbine succulenta*, gi30527334. Ximeniaceae: *Malania oleifera*, gi112408985. Zingiberaceae: *Amomum villosum*, gi257219599. Zygophyllaceae: *Larrea tridentata*, gi62902794.

Appendix B

18S and 26S Sequences from the 1KP Project Used in This Study

All sequences are available in the alignments in Dryad (doi:10.5061/dryad.bk827). The list is formatted as follows: family, binomial name, 1KP code.

18S: Aizoaceae, *Zaleya pentandra*, BERS; Aizoaceae, *Cypselea humifusa*, GJNX; Aizoaceae, *Sesuvium ventricosum*, OPZX; Amaranthaceae, *Atriplex hortensis*, AKTA; Amaranthaceae, *Blutoparon vermiculare*, CUTE; Amaranthaceae, *Aerva lanata*, EMIG; Amaranthaceae, *Alternanthera brasiliensis*, ENCD; Amaranthaceae, *Chenopodium quinoa*, SMMC; Apiaceae, *Centella asiatica*, WEQK; Asteraceae, *Flaveria cronquistii*, DSWR; Asteraceae, *Silybum Marianum*, EYKJ; Asteraceae, *Flaveria brownii*, LMXP; Asteraceae, *Matricaria matricarioides*, OAGK; Asteraceae, *Flaveria bidentis*, QBGG; Asteraceae, *Solidago canadensis*, TEZA; Asteraceae, *Flaveria angustifolia*, UQAZ; Asteraceae, *Flaveria bidentis*, ZNZC; Basellaceae, *Basella alba*, CTYH; Boraginaceae, *Heliotropium greggii*, ABEH; Cactaceae, *Lophophora williamsii*, CPKP; Calceolariaceae, *Calceolaria pinifolia*, DCCI; Cephalotaceae, *Cephalotus follicularis*, YZVJ; Cunoniaceae, *Cunonia capensis*, TIUZ; Curtisiaceae, *Curtisia dentata*, UZNH; Ericaceae, *Ledum palustre*, WXVX; Euphorbiaceae, *Chamaseyce mesebyranthemum*, LSLA; Exaceae, *Exacum affine*, KPUM; Fabaceae, *Copaifera officinalis*, RKLL; Fabaceae, *Wisteria floribunda*, RMWJ; Gentianaceae, *Gentiana acaulis*, ECTD; Lamiaceae, *Solenostemon scutellarioides*, BAHE; Lamiaceae, *Pycnanthemum tenuifolium*, DYFF; Lamiaceae, *Salvia* sp., EQDA; Lamiaceae, *Lawandula angustifolia*, FYUH; Loganiaceae, *Strychnos spinosa*, GGJD; Marcgraviaceae, *Souroubea ecauriculata*, BNTL; Melastomataceae, *Tetrazygia bicolor*, SWGX; Melianthaceae, *Greyia sutherlandii*, FONV; Melianthaceae, *Francoa appendiculata*, HDWF; Nothofagaceae, *Nothofagus obliqua*, TJLC; Nyctaginaceae, *Alliona* spp., EGOS; Nyctaginaceae, *Boerhavia* cf. *spiderwort*, MBWN; Onagraceae, *Epilobium* sp., FEDW; Orchidaceae, *Masdevallia yuangensis*, JSAG; Orchidaceae, *Platanthera clavellata*, MTHW; Orchidaceae, *Goodyera pubescens*, VTUS; Orobanchaceae, *Lindenbergia philippensis*, WUZV; Orobanchaceae, *Lindenbergia philippensis*, ZVFS; Pandanaceae, *Freylinetia multiflora*, DGXS; Papaveraceae, *Papaver rhoeas*, ACYX; Papaveraceae, *Papaver setigerum*, MLPX; Papaveraceae, *Papaver somniferum*, SUFP; Papaveraceae, *Eschscholzia*

californica, UNPT; Passifloraceae, *Malesherbia fasciculata*, COAQ; Physenaceae, *Physena madagascariensis*, RUUB; Poaceae, *Triodia* aff. *Byonei*, YXNR; Poaceae, *Panicum miliaceum*, SOHV; Poaceae, *Thyridolepis mitchelliana*, XBKS; Poaceae, *Neurachne munroi*, ZMGN; Primulaceae, *Maesa lanceolata*, OJCW; Primulaceae, *Jacquinia* sp., PTFA; Proteaceae, *Hakea prostata*, REOF; Quillajaceae, *Quillaja saponaria*, OQHZ; Rubiaceae, *Psychotria ipecacuanha*, JOPH; Rubiaceae, *Psychotria marginata*, PCNH; Salvadoraceae, *Salvadora* sp., RTTY; Saxifragaceae, *Bergenia* sp., CIAC; Scrophulariaceae, *Anticharis glandulosa*, EJBY; Simaroubaceae, *Quassia amara*, IKFD; Solanaceae, *Brugmansia sanguinea*, AIOU; Tecophilaeaceae, *Cyanastrum cordifolium*, RDYY; Xanthorrhoeaceae, *Phormium tenax*, FCEL; Xanthorrhoeaceae, *Aloe vera*, JVBR; Xanthorrhoeaceae, *Johnsonia pubescens*, WTDE.

26S: Aizoaceae, *Cypselea humifusa*, GJNX; Aizoaceae, *Sesuvium ventricosum*, OPZX; Aizoaceae, *Zaleya pentandra*, BERS; Alismataceae, *Sagittaria latifolia*, DWZT; Amaranthaceae, *Aerva lanata*, EMIG; Amaranthaceae, *Aerva lanata*, VKOE; Amaranthaceae, *Aerva persica*, GBCQ; Amaranthaceae, *Aerva persica*, MEAH; Amaranthaceae, *Alternanthera brasiliensis*, ENCD; Amaranthaceae, *Alternanthera brasiliensis*, KTQI; Amaranthaceae, *Alternanthera caracasana*, VUIT; Amaranthaceae, *Alternanthera caracasana*, WGUG; Amaranthaceae, *Alternanthera sessilis*, OYST; Amaranthaceae, *Alternanthera tenella*, DEMH; Amaranthaceae, *Amaranthus cruentus*, XSSD; Amaranthaceae, *Amaranthus retroflexus*, WMLW; Amaranthaceae, *Atriplex hortensis*, AKTA; Amaranthaceae, *Atriplex hortensis*, BDIW; Amaranthaceae, *Atriplex prostrata*, EPVF; Amaranthaceae, *Atriplex prostrata*, MUCT; Amaranthaceae, *Atriplex rosea*, LBZM; Amaranthaceae, *Atriplex rosea*, PDXY; Amaranthaceae, *Blutaparon vermiculare*, CUTE; Amaranthaceae, *Chenopodium quinoa*, SMMC; Amaryllidaceae, *Agapanthus africanus*, PRFO; Amborellaceae, *Amborella trichopoda*, URDJ; Anacardiaceae, *Rhus radicans*, YUOM; Apiaceae, *Centella asiatica*, WEQK; Apocynaceae, *Apocynum androsaemifolium*, UFQC; Apocynaceae, *Asclepias curassavica*, DSUV; Aquifoliaceae, *Ilex paraguariensis*, SXML; Aquifoliaceae, *Ilex* sp., DFYF; Arecaceae, *Sabal bermudana*, HWUP; Aristolochiaceae, *Aristolochia elegans*, PAWA; Asparagaceae, *Agave tequilana*, KXSK; Asparagaceae, *Lomandra longifolia*, MUMD; Asparagaceae, *Ruscus* sp., LSJW; Asparagaceae, *Sansevieria trifasciata*, MVRF; Asparagaceae, *Yucca brevifolia*, YBML; Asteraceae, *Carthamus lanatus*, CFRN; Asteraceae, *Erigeron speciosus*, DESP; Asteraceae, *Flaveria angustifolia*, EXHX; Asteraceae, *Flaveria angustifolia*, UQAZ; Asteraceae, *Flaveria bidentis*, QBGG; Asteraceae, *Flaveria bidentis*, ZNZC; Asteraceae, *Flaveria brownii*, IPUI; Asteraceae, *Flaveria brownii*, LMXP; Asteraceae, *Flaveria cronquistii*, DSWR; Asteraceae, *Flaveria cronquistii*, KJBH; Asteraceae, *Flaveria kochiana*, QXWF; Asteraceae, *Flaveria palmeri*, NVSO; Asteraceae, *Flaveria pringlei*, GFVW; Asteraceae, *Flaveria pringlei*, RZSW; Asteraceae, *Flaveria pubescens*, HXDV; Asteraceae, *Flaveria pubescens*, JZH; Asteraceae, *Flaveria trinervia*, HRVY; Asteraceae, *Flaveria trinervia*, RLCS; Asteraceae, *Matricaria matricarioides*, OAGK; Asteraceae, *Silybum marianum*, EYKJ; Asteraceae, *Solidago canadensis*, TEZA; Asteraceae, *Tragopogon dubius*, DDRL; Basellaceae, *Basella alba*, CTYH; Bataceae, *Batis maritima*, DZTK; Begoniaceae, *Begonia* sp., OCTM; Berberidaceae, *Podophyllum peltatum*, WFBF; Boraginaceae, *Ehretia acuminata*, EMAL; Boraginaceae, *Heliotropium greggii*, ABEH; Boraginaceae, *Heliotropium texanum*, CSWE; Boryaceae, *Borya sphaerocephala*, EMJJ; Brassicaceae, *Sinapis alba*, VMNH; Burseraceae, *Boswellia sacra*, FCCA; Cactaceae, *Lophophora williamsii*, CPKP; Calceolariaceae, *Calceolaria pinifolia*, DCCI; Caprifoliaceae, *Dipsacus sativum*, JTRM; Caprifoliaceae, *Symporicarpus* sp., CAQZ; Caprifoliaceae, *Valeriana officinalis*, FFFY; Cephalotaceae, *Cephalotus follicularis*, YZVJ; Cleomaceae, *Cleome gynandra*, ZLOA; Clusiaceae, *Garcinia livingstonei*, OSIP; Colchicaceae, *Colchicum autumnale*, NHIX; Combretaceae, *Terminalia neotaliala*, AJJE; Convolvulaceae, *Ipomoea indica*, OQBM; Convolvulaceae, *Ipomoea lobata*, IZNU; Convolvulaceae, *Ipomoea nil*, NHAG; Convolvulaceae, *Ipomoea pubescens*, EMBR; Convolvulaceae, *Ipomoea quamoclit*, ALUC; Coriariaceae, *Coriaria nepalensis*, NNGU; Cornaceae, *Alangium chinense*, FWBF; Crassulaceae, *Rhodiola rosea*, ZJUL; Cunoniaceae, *Cunonia capensis*, TIUZ; Curtisiaceae, *Curtisia dentata*, UZNH; Daphniphyllaceae, *Daphniphyllum macropodium*, FYTP; Diapensiaceae, *Galax urceolata*, UFHF; Dilleniaceae, *Dillenia indica*, EHNF; Ebenaceae, *Diospyros malabarica*, KVFU; Ericaceae, *Ledum palustre*, WXVX; Escalloniaceae, *Escallonia rubra*, CLMX; Euphorbiaceae, *Chamaesyce mesebyranthemum*, LSLA; Euphorbiaceae, *Euphorbia pekinensis*, PXYR; Euphorbiaceae, *Manihot grahamii*, XNLP; Eupomatiaceae, *Eupomatiopsis bennetti*, DHPO; Exaceae, *Exacum affine*, KPUM; Fabaceae, *Copaefera officinalis*, RKLL; Fabaceae, *Lupinus angustifolius*, TTRG; Fabaceae, *Wisteria floribunda*, RMWJ; Gentianaceae, *Gentiana acaulis*, ECTD; Gesneriaceae, *Saintpaulia ionantha*, RWKR; Gyrostemonaceae, *Gyrostemon ramulosus*, UAXP; Heliconiaceae, *Heliconia* sp., KNKV; Helwingiaceae, *Helwingia japonica*, QACK; Hernandiaceae, *Gyrocarpus americanus*, BSVG; Lamiaceae, *Agastache rugosa*, PUCW; Lamiaceae, *Lavandula angustifolia*, FYUH; Lamiaceae, *Pycnanthemum tenuifolium*, DYFF; Lamiaceae, *Salvia* spp., EQDA; Lamiaceae, *Solenostemon scutellarioides*, BAHE; Lamiaceae, *Vitex agnus*, DMLT; Lentibulariaceae, *Pinguicula agnata*, MXFG; Linaceae, *Linum grandiflorum*, MYVH; Loganiaceae, *Strychnos spinosa*, GGJD; Magnoliaceae, *Magnolia grandiflora*, WBOD; Malvaceae, *Hibiscus cannabinus*, OLXF; Marantaceae, *Maranta leuconeura*, JNUB; Marcgraviaceae, *Souroubea exauriculata*, BNTL; Melastomataceae, *Tetrazygia bicolor*, SWGX; Melianthaceae, *Francoa appendiculata*, HDWF; Melianthaceae, *Greyia sutherlandii*, FONV; Molluginaceae, *Mollugo cerviana*, RNBN; Molluginaceae, *Mollugo pentaphylla*, BZMI; Molluginaceae, *Mollugo pentaphylla*, HURS; Molluginaceae, *Mollugo verticillata*, QASA; Monimiaceae, *Peumus boldus*, KRJP; Moraceae, *Morus nigra*, XVJB; Moringaceae, *Moringa oleifera*, CZPV; Myrtaceae, *Syzygium paniculatum*, FDGU; Nothofagaceae, *Nothofagus obliqua*, TJLC; Nyctaginaceae, *Allionia* sp., EGOS; Nyctaginaceae, *Boerhavia* cf., MBWM; Nyctaginaceae, *Boerhavia dominii*, GDYP; Nyctaginaceae, *Bougainvillea spectabilis*, JAFJ; Nyctaginaceae, *Mirabilis jalapa*, DZRA; Nyctaginaceae, *Mirabilis jalapa*, GQAV; Nymphaeaceae, *Nuphar advena*, WTKZ; Ochnaceae, *Ochna serrulata*, CKDK; Onagraceae, *Epilobium* sp., FEDW; Onagraceae, *Oenothera affinis*, GVCB; Onagraceae, *Oenothera biennis*, MLUJ; Onagraceae, *Oenothera filiformis*, ECSL; Onagraceae, *Oenothera filiformis*, NQWS; Onagraceae, *Oenothera gaura*, IIFB; Onagraceae, *Oenothera gaura*, LHDP; Onagraceae, *Oenothera gaura*, TGOP; Onagraceae, *Oenothera grandiflora*, HOOU; Onagraceae, *Oenothera grandiflora*, REZJ;

Onagraceae, *Oenothera villaricae*, HKMQ; Orobanchaceae, *Conopholis americana*, FAMO; Orobanchaceae, *Lindenbergia philippensis*, WUZV; Orobanchaceae, *Lindenbergia philippensis*, ZVFS; Orobanchaceae, *Orobanche fasciculata*, PHOQ; Orobanchaceae, *Orobanche fasciculata*, VTOK; Oxalidaceae, *Oxalis* sp., JHCN; Paeoniaceae, *Paeonia lactiflora*, HTIP; Papaveraceae, *Argemone mexicana*, BFMT; Papaveraceae, *Argemone mexicana*, CCHG; Papaveraceae, *Argemone mexicana*, GOQJ; Papaveraceae, *Argemone mexicana*, YDEH; Papaveraceae, *Corydalis linstowiana*, ZGQD; Papaveraceae, *Eschscholzia californica*, NJKC; Papaveraceae, *Eschscholzia californica*, TUHA; Papaveraceae, *Eschscholzia californica*, UNPT; Papaveraceae, *Papaver bracteatum*, ZSCV; Papaveraceae, *Papaver rhoes*, ACYX; Papaveraceae, *Papaver rhoes*, IORZ; Papaveraceae, *Papaver setigerum*, FNKH; Papaveraceae, *Papaver setigerum*, MLPX; Papaveraceae, *Papaver somniferum*, BMRX; Papaveraceae, *Papaver somniferum*, MIKW; Papaveraceae, *Papaver somniferum*, SUFP; Passifloraceae, *Malesherbia fasciculata*, COAQ; Paulowniaceae, *Paulownia fargesii*, UMUL; Pentaphylacaceae, *Ternstroemia gymnanthera*, NGRR; Physenaceae, *Physena madagascariensis*, RUUB; Phytolaccaceae, *Phytolacca americana*, BKQU; Piperaceae, *Piper auritum*, MUNP; Poaceae, *Neurachne munroi*, ZMGN; Poaceae, *Panicum miliaceum*, SOHV; Poaceae, *Sorghum halapense*, EQWH; Poaceae, *Thyridolepis mitchelliana*, XBKS; Poaceae, *Thyridolepis multiculmis*, WCOR; Poaceae, *Triodia* aff., YXNR; Polemoniaceae, *Phlox* sp., FNEN; Polygonaceae, *Polygonum convolvulus*, FYSJ; Portulacaceae, *Portulaca mauli*, BYNZ; Portulacaceae, *Portulaca oleracea*, CZJT; Portulacaceae, *Portulaca oleracea*, TRLB; Posidoniaceae, *Posidonia australis*, BYQM; Primulaceae, *Jacquinia* sp., PTFA; Proteaceae, *Hakea prostrata*, OBOJ; Proteaceae, *Hakea prostrata*, REOF; Putranjivaceae, *Drypetes deplanchei*, RVGH; Rubiaceae, *Morinda citrifolia*, ULGV; Rubiaceae, *Psychotria ipecacuanha*, JOPH; Rubiaceae, *Psychotria marginata*, PCNH; Rutaceae, *Phelodendron amurense*, PGKL; Sabiaceae, *Meliosma cuneifolia*, AALA; Salicaceae, *Salix acutifolia*, INQX; Salicaceae, *Salix purpurea*, LFOG; Salicaceae, *Salix sachalinensis*, TDFT; Salicaceae, *Salix viminalis*, KKQD; Salvadoraceae, *Salvadora* sp., RTTY; Saxifragaceae, *Bergenia* sp., CIAC; Saxigrafaceae, *Saxifraga stolonifera*, FCBJ; Scrophulariaceae, *Anticharis glandulosa*, EJBY; Scrophulariaceae, *Buddleja lindleyana*, XRLM; Scrophulariaceae, *Buddleja* sp., GRFT; Scrophulariaceae, *Verbascum* sp., XXXA; Simaroubaceae, *Ailanthus altissima*, QICX; Simaroubaceae, *Quassia amara*, IKFD; Solanaceae, *Brugmansia sanguinea*, AIOU; Solanaceae, *Solanum sisymbriifolium*, NMDZ; Solanaceae, *Solanum xanthocarpum*, LQJY; Strelitziaceae, *Strelitzia reginae*, UOEL; Tecophilaeaceae, *Cyanastrum cordifolium*, RDYY; Trochodendraceae, *Trochodendron aralioides*, SWOH; Urticaceae, *Boehmeria nivea*, ACFP; Verbenaceae, *Verbena hastata*, GCFE; Vitaceae, *Tetrastigma vomerianum*, SZPD; Xanthorrhoeaceae, *Aloe vera*, JVBR; Xanthorrhoeaceae, *Hemerocallis* spp., BLAJ; Xanthorrhoeaceae, *Johnsonia pubescens*, WTDE; Xanthorrhoeaceae, *Phormium tenax*, FCEL.

Appendix C

Samples Used in the Combined 18S (62 1KP Samples) and 26S (134 1KP Samples) Data Set

Shown are accession numbers for GenBank sequences and four-letter codes for 1KP samples. The list is formatted as follows: 18S sample and 26S sample.

Acanthaceae *Justicia americana* gi4558879 and Acanthaceae *Justicia americana* gi19919606; Acoraceae *Acorus calamus* gi532564 and Acoraceae *Acorus calamus* gi66969242; Adoxaceae *Viburnum acerifolium* gi6689555 and Adoxaceae *Viburnum erosum* gi325071864; Aextoxicaceae *Aextoxicicon punctatum* gi7595359 and Aextoxicaceae *Aextoxicicon punctatum* gi22595012; Aizoaceae *Cypselea humifusa* GJNX and Aizoaceae *Cypselea humifusa* GJNX; Aizoaceae *Sesuvium ventricosum* OPZX and Aizoaceae *Sesuvium ventricosum* OPZX; Aizoaceae *Zaleya pentandra* BERS and Aizoaceae *Zaleya pentandra* BERS; Alismataceae *Alisma plantago-aquatica* gi6467915 and Alismataceae *Alisma plantago-aquatica* gi66969239; Alismataceae *Sagittaria trifolia* gi2346996 and Alismataceae *Sagittaria latifolia* DWZT; Alseuosmiaceae *Alseuosmia macrophylla* gi7595364 and Alseuosmiaceae *Alseuosmia* sp. DCT2010 gi305671600; Altingiaceae *Altingia* sp. Qiu 93006 gi1777674 and Altingiaceae *Altingia excelsa* gi19919649; Altingiaceae *Liquidambar styraciflua* gi1777684 and Altingiaceae *Liquidambar styraciflua* gi19919658; Amaranthaceae *Aerva lanata* EMIG and Amaranthaceae *Aerva lanata* EMIG; Amaranthaceae *Alternanthera brasiliensis* ENCD and Amaranthaceae *Alternanthera brasiliensis* ENCD; Amaranthaceae *Atriplex hortensis* AKTA and Amaranthaceae *Atriplex hortensis* AKTA; Amaranthaceae *Blutaparon vermiculare* CUTE and Amaranthaceae *Blutaparon vermiculare* CUTE; Amaranthaceae *Celosia argentea* gi7595403 and Amaranthaceae *Celosia argentea* gi19919535; Amaranthaceae *Chenopodium quinoa* SMMC and Amaranthaceae *Chenopodium quinoa* SMMC; Amaryllidaceae *Agapanthus africanus* gi313756773 and Amaryllidaceae *Agapanthus africanus* PRFO; Amborellaceae *Amborella trichopoda* gi1777635 and Amborellaceae *Amborella trichopoda* gi19919679; Amphorogynaceae *Leptomeria spinosa* gi149930362 and Amphorogynaceae *Leptomeria spinosa* gi149930373; Anacardiaceae *Rhus taitensis* gi290782502 and Anacardiaceae *Rhus radicans* YUOM; Anisophylleaceae *Anisophyllea fallax* gi33330855 and Anisophylleaceae *Anisophyllea fallax* gi62902783; Annonaceae *Asimina triloba* gi7595376 and Annonaceae *Asimina triloba* gi30527314; Annonaceae *Cananga odorata* gi22001094 and Annonaceae *Cananga odorata* gi110757088; Aphloiaceae *Aphloia theiformis* gi7595371 and Aphloiaceae *Aphloia theiformis* gi19919573; Apiaceae *Angelica gigas* gi200116396 and Apiaceae *Angelica lucida* gi37778823; Apiaceae *Apium graveolens* gi7595372 and Apiaceae *Apium graveolens* gi19919636; Apiaceae *Azorella caespitosa* gi305671582 and Apiaceae *Azorella fuegiana* gi37778834; Apiaceae *Centella asiatica* WEQK and Apiaceae *Centella asiatica* WEQK; Apiaceae *Mackinlaya confusa* gi305671589 and Apiaceae *Mackinlaya confusa* gi37778874; Apocynaceae *Apocynum* sp. Olmstead 256 gi4558882 and Apocynaceae *Apocynum androsaemifolium* UFQC; Apocynaceae *Asclepias syriaca* gi330441209 and Apocynaceae *Asclepias curassavica* DSUV; Apocynaceae *Nerium oleander* gi4558883 and Apocynaceae *Nerium oleander* gi19919619; Aquifoliaceae *Ilex opaca* gi6651251 and Aquifoliaceae *Ilex opaca* gi19919644; Araceae *Spathiphyllum wallisii* gi7595543 and Araceae *Spathiphyllum wallisii*

gi30527336; Araliaceae *Eleutherococcus senticosus* gi27544240 and Araliaceae *Eleutherococcus trifoliatus* gi37778857; Araliaceae *Hedera helix* gi1777644 and Araliaceae *Hedera helix* gi37778865; Araliaceae *Panax quinquefolius* gi2645181 and Araliaceae *Panax quinquefolius* gi37778890; Araliaceae *Polyscias ledermannii* gi290782414 and Araliaceae *Polyscias guilfoylei* gi37778894; Araliaceae *Schefflera macrostachya* gi290782413 and Araliaceae *Schefflera arboricola* gi37778900; Arecaceae *Sabal domingensis* gi12584253 and Arecaceae *Sabal bermudana* HWUP; Argophyllaceae *Corokia cotoneaster* gi1777654 and Argophyllaceae *Corokia cotoneaster* gi19919628; Aristolochiaceae *Aristolochia macrophylla* gi7595375 and Aristolochiaceae *Aristolochia macrophylla* gi30527313; Aristolochiaceae *Saruma henryi* gi532651 and Aristolochiaceae *Saruma henryi* gi66969232; Aristolochiaceae *Thottea tomentosa* gi66821900 and Aristolochiaceae *Thottea tomentosa* gi66969230; Asparagaceae *Agave ghiesbreghtii* gi313756767 and Asparagaceae *Agave tequilana* KXSK; Asparagaceae *Asparagus officinalis* gi283825474 and Asparagaceae *Asparagus officinalis* gi66969234; Asparagaceae *Lomandra hastilis* gi313756808 and Asparagaceae *Lomandra longifolia* MUMD; Asparagaceae *Ruscus aculeatus* gi313756727 and Asparagaceae *Ruscus* sp. LSJW; Asparagaceae *Sansevieria trifasciata* gi313756758 and Asparagaceae *Sansevieria trifasciata* MVRF; Asparagaceae *Yucca filamentosa* gi313756771 and Asparagaceae *Yucca brevifolia* YBML; Asteraceae *Barnadesia* sp. Palmer 180 gi4558886 and Asteraceae *Barnadesia caryophylla* gi19919687; Asteraceae *Flaveria angustifolia* UQAZ and Asteraceae *Flaveria angustifolia* UQAZ; Asteraceae *Flaveria bidentis* QBGG and Asteraceae *Flaveria bidentis* QBGG; Asteraceae *Flaveria bidentis* ZNZC and Asteraceae *Flaveria bidentis* ZNZC; Asteraceae *Flaveria brownii* LMXP and Asteraceae *Flaveria brownii* LMXP; Asteraceae *Flaveria cronquistii* DSWR and Asteraceae *Flaveria cronquistii* DSWR; Asteraceae *Matricaria matricarioides* OAGK and Asteraceae *Matricaria matricarioides* OAGK; Asteraceae *Silybum marianum* EYKJ and Asteraceae *Silybum marianum* EYKJ; Asteraceae *Solidago canadensis* TEZA and Asteraceae *Solidago canadensis* TEZA; Asteraceae *Tragopogon dubius* gi1777648 and Asteraceae *Tragopogon dubius* DDRL; Asteropeiaceae *Asteropeia micraster* gi7595377 and Asteropeiaceae *Asteropeia micraster* gi19919531; Atherospermataceae *Atherosperma moschatum* gi6467908 and Atherospermataceae *Atherosperma moschatum* gi66969216; Austrobaileyaceae *Austrobaileya scandens* gi1022919 and Austrobaileyaceae *Austrobaileya scandens* gi30527315; Balsaminaceae *Impatiens pallida* gi2924749 and Balsaminaceae *Impatiens repens* gi19919595; Barbeyaceae *Barbeya oleoides* gi336239075 and Barbeyaceae *Barbeya oleoides* gi336239101; Basellaceae *Basella alba* CTYH and Basellaceae *Basella alba* CTYH; Bataceae *Batis maritima* gi1777639 and Bataceae *Batis maritima* DZTK; Begoniaceae *Begonia oxyloba* gi2735769 and Begoniaceae *Begonia oxyloba* gi66276233; Berberidaceae *Berberis bealei* gi256373698 and Berberidaceae *Berberis bealei* gi66969201; Berberidaceae *Caulophyllum thalictroides* gi1369766 and Berberidaceae *Caulophyllum thalictroides* gi22595013; Berberidaceae *Nandina domestica* gi904137 and Berberidaceae *Nandina domestica* gi22595014; Berberidaceae *Podophyllum peltatum* gi532633 and Berberidaceae *Podophyllum peltatum* gi66969202; Berberidopsidaceae *Berberidopsis corallina* gi7595386 and Berberidopsidaceae *Berberidopsis corallina* gi22595015; Betulaceae *Alnus glutinosa* gi15990 and Betulaceae *Alnus glutinosa* gi19919547; Bixaceae *Bixa orellana* gi7595388 and Bixaceae *Bixa orellana* gi19919670; Boraginaceae *Borago officinalis* gi4558891 and Boraginaceae *Borago officinalis* gi19919620; Boraginaceae *Ehretia acuminata* gi334691676 and Boraginaceae *Ehretia acuminata* EMAL; Boraginaceae *Heliotropium greggii* ABEH and Boraginaceae *Heliotropium greggii* ABEH; Boryaceae *Borya septentrionalis* gi313756823 and Boryaceae *Borya sphaerocephala* EMJJ; Brassicaceae *Sinapis alba* gi21157 and Brassicaceae *Sinapis alba* gi19919583; Buxaceae *Didymelis perrieri* gi6706954 and Buxaceae *Didymelis perrieri* gi22595020; Buxaceae *Pachysandra procumbens* gi6706946 and Buxaceae *Pachysandra procumbens* gi22595017; Cabombaceae *Cabomba caroliniana* gi4406189 and Cabombaceae *Cabomba caroliniana* gi19919680; Cactaceae *Lophophora williamsii* CPKP and Cactaceae *Lophophora williamsii* CPKP; Cactaceae *Pereskia aculeata* gi7595506 and Cactaceae *Pereskia aculeata* gi19919533; Calceolariaceae *Calceolaria pinifolia* DCCI and Calceolariaceae *Calceolaria pinifolia* DCCI; Calycanthaceae *Calycanthus chinensis* gi94450843 and Calycanthaceae *Calycanthus occidentalis* gi30527317; Calycanthaceae *Chimonanthus praecox* gi20799689 and Calycanthaceae *Chimonanthus praecox* gi66969220; Calyceraceae *Boopis graminea* gi4558894 and Calyceraceae *Boopis graminea* gi19919625; Campanulaceae *Campanula ramulosa* gi1777643 and Campanulaceae *Campanula trachelium* gi19919632; Campanulaceae *Codonopsis pilosula* gi4558895 and Campanulaceae *Codonopsis pilosula* gi19919631; Canellaceae *Canella winterana* gi7595399 and Canellaceae *Canella winterana* gi30527318; Canellaceae *Cinnamodendron ekmanii* gi7595407 and Canellaceae *Cinnamodendron* sp. MJZ2002 gi30527321; Cannabaceae *Cannabis sativa* gi336239077 and Cannabaceae *Cannabis sativa* gi157689139; Capparaceae *Capparis spinosa* gi156446066 and Capparaceae *Capparis sandwichiana* gi19919581; Caprifoliaceae *Diervilla sessilifolia* gi305671587 and Caprifoliaceae *Diervilla sessilifolia* gi305671604; Caprifoliaceae *Dipelta yunnanensis* gi305671588 and Caprifoliaceae *Dipelta yunnanensis* gi305671605; Caprifoliaceae *Dipsacus asperoides* gi260751524 and Caprifoliaceae *Dipsacus sativus* JTRM; Caprifoliaceae *Lonicera maackii* gi1857127 and Caprifoliaceae *Lonicera japonica* gi305671608; Caprifoliaceae *Scabiosa* sp. Albach 39 gi6689362 and Caprifoliaceae *Scabiosa* sp. Albach 39 gi19919639; Caprifoliaceae *Symporicarpos albus* gi1777647 and Caprifoliaceae *Symporicarpos albus* gi19919683; Caprifoliaceae *Triplostegia glandulifera* gi305671598 and Caprifoliaceae *Triplostegia glandulifera* gi305671614; Caprifoliaceae *Valeriana officinalis* gi6689554 and Caprifoliaceae *Valeriana officinalis* gi19919640; Caprifoliaceae *Zabelia triflora* gi6686862 and Caprifoliaceae *Zabelia triflora* gi19919641; Cardiopteridaceae *Gonocaryum litorale* gi7595439 and Cardiopteridaceae *Gonocaryum litorale* gi19919642; Caryophyllaceae *Stellaria media* gi7595547 and Caryophyllaceae *Stellaria media* gi19919525; Celastraceae *Brexia madagascariensis* gi1777675 and Celastraceae *Brexia madagascariensis* gi19919553; Celastraceae *Euonymus alatus* gi51320367 and Celastraceae *Euonymus alatus* gi19919554; Celastraceae *Loeseneriella barbata* gi7595448 and Celastraceae *Loeseneriella barbata* gi19919552; Celastraceae *Stackhousia minima* gi7595546 and Celastraceae *Stackhousia minima* gi19919555; Centroplacaceae *Bhesa robusta* gi62907003 and Centroplacaceae *Bhesa robusta* gi62902770; Cephalotaceae *Cephalotus follicularis* YZVJ and Cephalotaceae *Cephalotus*

follicularis YZVJ; Ceratophyllaceae *Ceratophyllum demersum* gi1777656 and Ceratophyllaceae *Ceratophyllum demersum* gi19919669; Ceratophyllaceae *Ceratophyllum submersum* gi6467912 and Ceratophyllaceae *Ceratophyllum submersum* gi66969210; Chloranthaceae *Chloranthus multistachys* gi7595405 and Chloranthaceae *Chloranthus multistachys* gi30527320; Chloranthaceae *Hedyosmum arborescens* gi1022977 and Chloranthaceae *Hedyosmum arborescens* gi19919667; Chloranthaceae *Sarcandra glabra* gi6706949 and Chloranthaceae *Sarcandra chloranthoides* gi66969243; Chrysobalanaceae *Chrysobalanus icaco* gi1777660 and Chrysobalanaceae *Chrysobalanus icaco* gi19919560; Circaeasteraceae *Circaeaster agrestis* gi6706951 and Circaeasteraceae *Circaeaster agrestis* gi22595019; Circaeasteraceae *Kingdonia uniflora* gi6706950 and Circaeasteraceae *Kingdonia uniflora* gi22595018; Cleomaceae *Cleome hassleriana* gi1777642 and Cleomaceae *Cleome gynandra* ZLOA; Clusiaceae *Garcinia latissima* gi261873442 and Clusiaceae *Garcinia livingstonei* OSIP; Colchicaceae *Colchicum autumnale* gi2795838 and Colchicaceae *Colchicum autumnale* NHIX; Columelliaceae *Desfontainia spinosa* gi305671586 and Columelliaceae *Desfontainia spinosa* gi305671603; Combretaceae *Terminalia catappa* gi7595557 and Combretaceae *Terminalia neotaliala* AJJE; Connaraceae *Connarus championii* gi62907030 and Connaraceae *Connarus championii* gi62902786; Convolvulaceae *Convolvulus arvensis* gi6687109 and Convolvulaceae *Convolvulus arvensis* gi19919617; Convolvulaceae *Ipomoea batatas* gi295883878 and Convolvulaceae *Ipomoea nil* NHAG; Coriariaceae *Coriaria arborea* gi2735773 and Coriariaceae *Coriaria nepalensis* NNGU; Cornaceae *Alangium chinense* gi7595363 and Cornaceae *Alangium chinense* gi30230577; Cornaceae *Camptotheca acuminata* gi1777691 and Cornaceae *Camptotheca acuminata* gi30230579; Cornaceae *Cornus officinalis* gi1698485 and Cornaceae *Cornus officinalis* gi15284139; Cornaceae *Davidia involucrata* gi6687372 and Cornaceae *Davidia involucrata* gi30230582; Cornaceae *Nyssa ogeche* gi1698486 and Cornaceae *Nyssa ogeche* gi15284148; Corynocarpaceae *Corynocarpus laevigata* gi290782436 and Corynocarpaceae *Corynocarpus laevigata* gi19919551; Crassulaceae *Crassula marnierana* gi1777662 and Crassulaceae *Crassula marnierana* gi19919651; Crossosomataceae *Crossosoma californicum* gi1777655 and Crossosomataceae *Crossosoma californicum* gi19919572; Crypteroniaceae *Crypteronia paniculata* gi133918014 and Crypteroniaceae *Crypteronia paniculata* gi157689140; Cucurbitaceae *Cucurbita pepo* gi7595415 and Cucurbitaceae *Cucurbita pepo* gi19919549; Cunoniaceae *Cunonia capensis* TIUZ and Cunoniaceae *Cunonia capensis* TIUZ; Cunoniaceae *Davidsonia pruriens* gi7595417 and Cunoniaceae *Davidsonia pruriens* gi62902788; Curtisiaceae *Curtisia dentata* UZNH and Curtisiaceae *Curtisia dentata* UZNH; Cyclanthaceae *Carludovica palmata* gi15428392 and Cyclanthaceae *Carludovica palmata* gi66969236; Daphniphyllaceae *Daphniphyllum* sp. Qiu 91026 gi1777665 and Daphniphyllaceae *Daphniphyllum macropodium* FYTP; Daticaceae *Datisca cannabina* gi2735771 and Daticaceae *Datisca cannabina* gi66276240; Degeneriaceae *Degeneria vitiensis* gi7595418 and Degeneriaceae *Degeneria vitiensis* gi66969225; Diapensiaceae *Galax urceolata* gi18654243 and Diapensiaceae *Galax urceolata* UFHF; Dilleniaceae *Dillenia alata* gi1049330 and Dilleniaceae *Dillenia indica* EHNF; Dilleniaceae *Tetracera asiatica* gi19919538 and Dilleniaceae *Tetracera asiatica* gi6689361; Dioncophyllaceae *Triphyophyllum peltatum* gi7595569 and Dioncophyllaceae *Triphyophyllum peltatum* gi19919532; Dioscoreaceae *Tacca chantieri* gi116282763 and Dioscoreaceae *Tacca chantieri* gi30527337; Dipentodontaceae *Perrottetia longistylis* gi62907019 and Dipentodontaceae *Perrottetia longistylis* gi62902781; Droseraceae *Drosera capensis* gi1777664 and Droseraceae *Drosera capensis* gi22595021; Ebenaceae *Diospyros ferrea* gi290782444 and Ebenaceae *Diospyros malabarica* KVFU; Elaeagnaceae *Elaeagnus bockii* gi336239083 and Elaeagnaceae *Elaeagnus bockii* gi336239107; Elaeagnaceae *Hippophae rhamnoides* subsp. *sinensis* gi336239087 and Elaeagnaceae *Hippophae rhamnoides* subsp. *sinensis* gi336239111; Elaeocarpaceae *Sloanea latifolia* gi1777733 and Elaeocarpaceae *Sloanea berteroana* gi19919567; Ephedraceae *Ephedra sinica* gi257075173 and Ephedraceae *Ephedra distachya* gi2687429; Ericaceae *Ledum palustre* WXVX and Ericaceae *Ledum palustre* WXVX; Ericaceae *Vaccinium macrocarpon* gi33312053 and Ericaceae *Vaccinium reticulatum* gi284159172; Erythroxylaceae *Erythroxylum confusum* gi7595429 and Erythroxylaceae *Erythroxylum coca* gi133900039; Escalloniaceae *Escallonia coquimbensis* gi1777678 and Escalloniaceae *Escallonia coquimbensis* gi305671606; Euphorbiaceae *Acalypha californica* gi51320343 and Euphorbiaceae *Acalypha californica* gi133900033; Euphorbiaceae *Chamaseyce mesebyranthemum* LSLA and Euphorbiaceae *Chamaseyce mesebyranthemum* LSLA; Euphorbiaceae *Dalechampia spathulata* gi119368144 and Euphorbiaceae *Dalechampia spathulata* gi133900037; Euphorbiaceae *Endospermum moluccanum* gi51320366 and Euphorbiaceae *Endospermum moluccanum* gi133900038; Euphorbiaceae *Euphorbia pulcherrima* gi1777679 and Euphorbiaceae *Euphorbia pekinensis* PXYR; Euphorbiaceae *Manihot grahamii* gi257853457 and Euphorbiaceae *Manihot grahamii* XNLP; Euphorbiaceae *Neoscorchedinia kingii* gi51320390 and Euphorbiaceae *Neoscorchedinia kingii* gi133900040; Eupomatiaceae *Eupomatiopsis bennetti* gi22001095 and Eupomatiaceae *Eupomatiopsis bennetti* DHPO; Eupteleaceae *Euptelea polyandra* gi1478053 and Eupteleaceae *Euptelea polyandra* gi22595022; Fabaceae *Glycine max* gi18729 and Fabaceae *Glycine max* gi62902790; Fabaceae *Wisteria floribunda* RMWJ and Fabaceae *Wisteria floribunda* RMWJ; Fagaceae *Chrysolepis sempervirens* gi7595406 and Fagaceae *Chrysolepis sempervirens* gi19919548; Fouquieriaceae *Fouquieria columnaris* gi2735713 and Fouquieriaceae *Fouquieria columnaris* gi19919600; Garryaceae *Aucuba japonica* gi1777652 and Garryaceae *Aucuba japonica* gi325071865; Garryaceae *Garrya elliptica* gi1777680 and Garryaceae *Garrya elliptica* gi19919622; Gentianaceae *Exacum affine* KPUM and Gentianaceae *Exacum affine* KPUM; Gentianaceae *Gentiana acaulis* ECTD and Gentianaceae *Gentiana acaulis* ECTD; Geraniaceae *Geranium himalayense* gi11066015 and Geraniaceae *Geranium sanguineum* gi19919570; Gesneriaceae *Rhynchoglossum notonianum* gi6689109 and Gesneriaceae *Rhynchoglossum notonianum* gi19919605; Ginkgoaceae *Ginkgo biloba* gi556508 and Ginkgoaceae *Ginkgo biloba* gi170516003; Gnetaceae *Gnetum gnemon* gi56069878 and Gnetaceae *Gnetum gnemon* gi2687428; Gomortegaceae *Gomortega keule* gi156622740 and Gomortegaceae *Gomortega keule* gi30527323; Goodeniaceae *Scaevola aemula* gi6689107 and Goodeniaceae *Scaevola auriculata* gi305671612; Griseliniaceae *Griselinia lucida* gi290782437 and Griseliniaceae *Griselinia lucida* gi37778863; Grossulariaceae *Ribes aureum* gi532227 and Grossulariaceae *Ribes speciosum* gi19919655; Gunneraceae *Gunnera hamiltonii*

gi19919645 and Gunneraceae *Gunnera hamiltonii* gi19919645; Gunneraceae *Gunnera manicata* gi22595023 and Gunneraceae *Gunnera manicata* gi22595023; Gyrostemonaceae *Gyrostemon tepperi* gi3265095 and Gyrostemonaceae *Gyrostemon ramulosus* UAXP; Haloragaceae *Haloragis erecta* gi6706960 and Haloragaceae *Haloragis aspera* gi19919650; Hamamelidaceae *Corylopsis pauciflora* gi6706961 and Hamamelidaceae *Corylopsis pauciflora* gi19919654; Hamamelidaceae *Disanthus cercidifolius* gi6706962 and Hamamelidaceae *Disanthus cercidifolius* gi19919659; Hamamelidaceae *Exbucklandia populnea* gi6706963 and Hamamelidaceae *Exbucklandia populnea* gi19919660; Hamamelidaceae *Rhodoleia championii* gi9502205 and Hamamelidaceae *Rhodoleia* sp. DES2002 gi19919677; Heliconiaceae *Heliconia indica* gi2795847 and Heliconiaceae *Heliconia* sp. KNKV; Helwingiaceae *Helwingia japonica* gi1777668 and Helwingiaceae *Helwingia japonica* QACK; Hernandiaceae *Gyrocarpus americanus* gi7595443 and Hernandiaceae *Gyrocarpus americanus* BSVG; Hernandiaceae *Hernandia ovigera* gi66821901 and Hernandiaceae *Hernandia nymphaeifolia* gi30527325; Himantandraceae *Galbulimima belgraveana* gi7595436 and Himantandraceae *Galbulimima belgraveana* gi22595024; Hippocastanaceae *Aesculus pavia* gi7595358 and Hippocastanaceae *Aesculus pavia* gi19919579; Humiriaceae *Humiria balsamifera* gi62907031 and Humiriaceae *Humiria balsamifera* gi62902791; Hydrangeaceae *Carpenteria californica* gi6687108 and Hydrangeaceae *Carpenteria californica* gi325071839; Hydrangeaceae *Decumaria barbara* gi6687371 and Hydrangeaceae *Decumaria barbara* gi325071840; Hydrangeaceae *Hydrangea macrophylla* gi1777693 and Hydrangeaceae *Hydrangea macrophylla* gi325071848; Hydrangeaceae *Philadelphus lewisi* gi1777703 and Hydrangeaceae *Philadelphus lewisi* gi22595025; Hydroleaceae *Hydrolea ovata* gi6687735 and Hydroleaceae *Hydrolea ovata* gi19919618; Hypericaceae *Hypericum perforatum* gi7595454 and Hypericaceae *Hypericum perforatum* gi19919563; Iteaceae *Itea virginica* gi1777683 and Iteaceae *Itea virginica* gi19919657; Juglandaceae *Juglans nigra* gi7595463 and Juglandaceae *Juglans nigra* gi19919546; Krameriacae *Krameria ixine* gi7595468 and Krameriacae *Krameria ixine* gi19919557; Lacistemaecae *Lacistema aggregatum* gi118918056 and Lacistemaecae *Lacistema aggregatum* gi62902792; Lactoridaceae *Lactoris fernandeziana* gi1777695 and Lactoridaceae *Lactoris fernandeziana* gi30527326; Lamiaceae *Lavandula angustifolia* FYUH and Lamiaceae *Lavandula angustifolia* FYUH; Lamiaceae *Salvia* sp. 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Coode 7925 gi19919594; Thymelaeaceae *Thymelaea hirsuta* gi7595561 and Thymelaeaceae *Thymelaea hirsuta* gi19919675; Tofieldiaceae *Plea tenuifolia* gi7595515 and Tofieldiaceae *Plea tenuifolia* gi30527335; Tofieldiaceae *Tofieldia calyculata* gi7595563 and Tofieldiaceae *Tofieldia calyculata* gi66969241; Torricelliaceae *Melanophylla alnifolia* gi6688633 and Torricelliaceae *Melanophylla alnifolia* gi37778877; Trochodendraceae *Trochodendron aralioides* gi1777734 and Trochodendraceae *Trochodendron aralioides* gi19919646; Tropaeolaceae *Tropaeolum majus* gi598415 and Tropaeolaceae *Tropaeolum tricolor* gi19919585; Ulmaceae *Celtis tetrandra* gi336239078 and Ulmaceae *Celtis tetrandra* gi336239102; Ulmaceae *Celtis yunnanensis* gi1777724 and Ulmaceae *Celtis yunnanensis* gi19919539; Ulmaceae *Ulmus macrocarpa* gi336239094 and Ulmaceae *Ulmus macrocarpa* gi336239118; Ulmaceae *Zelkova serrata* gi1777739 and Ulmaceae *Zelkova serrata* gi19919540; Urticaceae *Boehmeria nivea* gi7595390 and Urticaceae *Boehmeria nivea* ACFP; Urticaceae *Debregeasia saeneb* gi336239080 and Urticaceae *Debregeasia saeneb* gi336239104; Urticaceae *Pilea cadierei* gi1777731 and Urticaceae *Pilea cadierei* gi336239114; Vahliaeae *Vahlia capensis* gi1777738 and Vahliaeae *Vahlia capensis* gi19919623; Verbenaceae *Verbena bracteata* gi6689556 and Verbenaceae *Verbena hastata* GCFE; Violaceae *Rinorea pubiflora* gi62907035 and Violaceae *Rinorea pubiflora* gi62902797; Viscaceae *Viscum album* gi1777737 and Viscaceae *Viscum album* gi22595048; Vitaceae *Tetrastigma hypoglaucum* gi51320408 and Vitaceae *Tetrastigma voinierianum* SZPD; Vitaceae *Vitis* sp. Soltis & Soltis 2519 gi7595573 and Vitaceae *Vitis aestivalis* gi19919648; Vivianiaceae *Viviana marifolia* gi7595574 and Vivianiaceae *Viviana marifolia* gi19919571; Welwitschiaceae *Welwitschia mirabilis* gi2588925 and Welwitschiaceae *Welwitschia mirabilis* gi110757094; Winteraceae *Takhtajania perrieri* gi7595552 and Winteraceae *Takhtajania perrieri* gi66969233; Winteraceae *Tasmannia insipida* gi7595555 and Winteraceae *Tasmannia insipida* gi30527332; Xanthorrhoeaceae *Aloe vera* JVBR and Xanthorrhoeaceae *Aloe vera* JVBR; Xanthorrhoeaceae *Bulbine succulenta* gi7595396 and Xanthorrhoeaceae *Bulbine succulenta* gi30527334; Xanthorrhoeaceae *Hemerocallis minor* gi313756827 and

Xanthorrhoeaceae *Hemerocallis* spp. BLAJ; Xanthorrhoeaceae *Johnsonia pubescens* WTDE and Xanthorrhoeaceae *Johnsonia pubescens* WTDE; Xanthorrhoeaceae *Phormium tenax* FCEL and Xanthorrhoeaceae *Phormium tenax* FCEL; Zygophyllaceae *Larrea tridentata* gi62907034 and Zygophyllaceae *Larrea tridentata* gi62902794.

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