

MOLECULAR PHYLOGENETICS

A molecular phylogeny of the Solanaceae

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A phylogeny of Solanaceae is presented based on the chloroplast DNA regions *ndhF* and *trnLF*. With 89 genera and 190 species included, this represents a nearly comprehensive genus-level sampling and provides a framework phylogeny for the entire family that helps integrate many previously-published phylogenetic studies within Solanaceae. The four genera comprising the family Goetzeaceae and the monotypic families Duckeodendraceae, Nolanaceae, and Sclerophylaceae, often recognized in traditional classifications, are shown to be included in Solanaceae. The current results corroborate previous studies that identify a monophyletic subfamily Solanoideae and the more inclusive “ $x = 12$ ” clade, which includes *Nicotiana* and the Australian tribe Anthocercideae. These results also provide greater resolution among lineages within Solanoideae, confirming *Jaltomata* as sister to *Solanum* and identifying a clade comprised primarily of tribes Capsiceae (*Capsicum* and *Lycianthes*) and Physaleae. Stronger evidence also is provided for the inclusion of *Capsicum* within a paraphyletic *Lycianthes*. Solanaceae are a predominantly New World group, with several lineages represented on other continents. Apart from events within *Solanum* (for which sampling in this study is inadequate for biogeographic interpretations) the Old World representatives of Solanaceae can be accounted for by eight or nine dispersal events.

KEYWORDS: biogeography, chloroplast DNA, chromosome evolution, *ndhF*, phylogeny, Solanaceae, *trnLF*

INTRODUCTION

Assigned to Solanales (APG II, 2003) along with Convolvulaceae, Hydroleaceae, Montiniaceae, and Sphenocleaceae, Solanaceae are a monophyletic group containing approximately 100 genera and 2,500 species (D’Arcy, 1991; Olmstead & al., 1999; Hunziker, 2001; Olmstead & Bohs, 2007). Species of Solanaceae occur on all temperate and tropical continents, but by far the greatest biodiversity of the family is found in the western hemisphere. The Solanaceae include many of the world’s most important agricultural species, including potatoes, tomatoes, eggplants, chili peppers, tomatillos, tobacco, petunia, and several other crops of regional significance. Due, in part,

to their tremendous economic importance, Solanaceae have been subject to much systematic and other biological research, exemplified by the six international conferences and resulting volumes (Hawkes & al., 1979, 1991; D’Arcy, 1986b; Nee & al., 1999; Van den Berg & al., 2001; Spooner & al., 2007), and a monographic treatment of the family, culminating a lifetime’s work by Armando Hunziker and his colleagues (Hunziker, 2001).

Traditional classifications of the family typically recognized two subfamilies, Cestroideae and Solanoideae (D’Arcy, 1979, 1991; Hunziker, 1979, 2001; Olmstead & Palmer 1992). An additional subfamily, Nolanoideae, has been segregated by some taxonomists as a distinct family, Nolanaceae (Cronquist, 1981; Thorne, 1992; Hunziker, 2001). Subfamily Solanoideae was considered to be ancestral within the Solanaceae and was characterized by its curved embryos contained in flattened discoid seeds and typically berry-like fruits (D’Arcy, 1979; Hunziker, 1979). Subfamily Cestroideae, with its straight or somewhat bent embryos in small, angular to subglobose seeds

This paper is dedicated to the memory of William D’Arcy and Armando Hunziker, two scholars of the family, to whom we owe a debt of gratitude for advancing our understanding of the Solanaceae.

and typically capsular fruits, was presumed to be derived. However, two recent classifications have been proposed for the family that deviate from these traditional views (Olmstead & al., 1999; Hunziker, 2001). Hunziker's classification (Hunziker, 2001), based mainly on morphology with a secondary emphasis on chemistry, reflects traditional views with some modifications over past treatments. For example, his linear order was designed to reflect "increasing complexity", and may be inferred to represent an approximate evolutionary sequence. In this regard it is interesting to note that he began his sequence with Cestroideae, which is the reverse of the order presented previously (Hunziker, 1979), suggesting that some of what had been learned about phylogeny influenced his ideas. However, he still retained *Schizanthus* and Salpiglossideae, with their bilateral symmetry, and Anthocercideae at the end of the sequence. He also recognized four small subfamilies (Anthocercidoideae, Juanulloideae, Salpiglossoidae, Schizanthoideae) in addition to the two large ones, Cestroideae and Solanoideae, and several small tribes or subtribes for individual genera that have been shown in phylogenetic studies (e.g., Olmstead & al., 1999) to be isolated from other recognized groups. He excluded genera such as *Duckeodendron*, *Nolana*, *Sclerophylax*, *Goetzea*, *Espadaea*, *Coeloneurum*, *Henoonia*, and *Tsoala* from the Solanaceae, placing some of them in segregate families.

Since the early 1990's, phylogenetic relationships within Solanaceae have been examined using molecular characters, particularly chloroplast DNA sequence data (Olmstead & Palmer, 1992; Spooner & al., 1993; Olmstead & Sweere, 1994; Fay & al. 1998; Olmstead & al. 1999; Gemeinholzer & Wink, 2001; Santiago-Valentin & Olmstead, 2003; Clarkson & al. 2004; Bohs, 2005; Levin & al., 2005, 2006; Weese & Bohs, 2007), and these findings have challenged previous views. Nolanaceae has been shown to be nested within the Solanaceae (Olmstead & Palmer, 1992; Tago-Nakazawa & Dillon, 1999). Several other taxa traditionally excluded from Solanaceae (*Goetzea* and related genera, *Duckeodendron*, *Sclerophylax*) were found to be derived from within Solanaceae (Olmstead & al., 1999; Gemeinholzer & Wink, 2001; Santiago-Valentin & Olmstead, 2003). Subfamilies Solanoideae and Cestroideae as traditionally circumscribed have been shown to be non-monophyletic, with Cestroideae paraphyletic relative to Solanoideae, and Solanoideae, in turn, paraphyletic relative to Nolanaceae. An important and previously unrecognized group consisting of subfamily Solanoideae (including *Nolana*), tribe Anthocercideae (endemic to Australia) and *Nicotiana*, all united by a base chromosome number of 12, was identified and referred to as the "x = 12" clade (Olmstead & Sweere, 1994). Several genera (*Cyphomandra*, *Lycopersicon*, *Normania*, *Triguera*) have been shown to belong within *Solanum* (Olmstead

& Palmer, 1992; Spooner & al., 1993; Bohs & Olmstead, 2001). However, many details of the phylogeny have remained obscure due to sparse taxonomic sampling and the limited resolving power of the DNA regions studied. In this study we expand both taxonomic and DNA sequence sampling to produce a more comprehensive and better-resolved phylogeny.

While the results presented here are based on cpDNA sequences, the use of nuclear gene sequences, particularly the Granule-Bound Starch Synthase gene (*GBSSI*, or *waxy*) has been used in several studies in Solanaceae (Peralta & Spooner, 2001; Walsh & Hoot, 2001; Levin & Miller, 2005; Levin & al., 2005, 2006; Smith & Baum, 2006; Yuan & al., 2006; Weese & Bohs, 2007) and may provide a useful dataset for the entire Solanaceae for comparison with cpDNA sequences. Also, a novel nuclear gene for phylogenetic reconstruction, Salicylic Acid Methyltransferase (*SAMT*) has been applied to a family-wide study (Martins & Barkman, 2005). A summary of molecular systematic studies of Solanaceae is found in Olmstead & Bohs (2007).

MATERIALS AND METHODS

A total of 195 taxa was included in this study (Appendix) including five outgroup taxa, four from the sister clade Convolvulaceae (*Convolvulus*, *Dinetus*, *Evolvulus*, and *Ipomoea*), and *Montinia* (Montiniaceae), a more distant relative within Solanales (Olmstead & al., 2000; Bremer & al., 2002; Stefanovic & al., 2002). A goal was to sample genus-level diversity as completely as possible, including multiple species of all the larger genera. However, sufficient sampling to test hypotheses of monophyly at the generic level was largely beyond the scope of this study. Multiple accessions of a few species were included to confirm sequences when unanticipated results were obtained (e.g., *Protoschwenkia*, *Latua*) and are included in the Appendix, even though only one accession was included in the analyses. Similarly, multiple accessions of two species (*Atropa belladonna*, *Markea panamensis*) were collected under different names, now recognized as synonyms, and from different parts of the species distribution and both were included to confirm the taxonomy. The recent classification of Hunziker (2001) included 92 genera, of which 85 were sampled here, along with seven genera that were excluded from Solanaceae by him (*Duckeodendron*, *Espadaea*, *Goetzea*, *Henoonia*, *Nolana*, *Sclerophylax*, *Tsoala*). A summary of molecular phylogenetic studies of Solanaceae (Olmstead & Bohs, 2007) recognized 98 genera, of which 89 are sampled here. All taxa listed in the Appendix have sequence data for *ndhF*, whereas *trnLF* sequences are missing for five species (*Jaltomata sinuosa*, *Capsicum pubescens*, *Mellissia begoniifolia*, *Nierembergia andina*,

Benthamiella skottsbergii). For the latter, *ndhF* sequences were obtained either from taxa for which only a small amount of DNA was obtained from a herbarium specimen and *trnLF* sequencing failed (e.g., *Benthamiella*), or were sequenced as part of another study and DNA was not available for this study (e.g., *Mellissia*, kindly provided by Q. Cronk). In a few other cases (four accessions each for *ndhF* and *trnLF*, but never for the same species), only half of one or the other of the gene regions was included for similar reasons (*Cyphanthera anthocercidea*, *Larnax subtriflora*, *Nicotiana glauca*, *N. africana* for *ndhF*; *Athenaea* sp., *Dunalia solanacea*, *Nothoestrum latifolium*, *Sclerophylax giliesii* for *trnLF*). A total of 145 previously published sequences was included along with 245 new sequences obtained for this study.

DNA was obtained from fresh plant tissue, field-collected, silica-gel dried tissues, and herbarium specimens. Contributions from numerous other Solanaceae systematists and Botanical Gardens are gratefully acknowledged. Sequences were obtained by direct sequencing of PCR products following protocols described previously (Olmstead & Sweere, 1994; Olmstead & Reeves, 1995; Santiago-Valentin & Olmstead, 2003; Bohs, 2004). Sequences were aligned by eye and adjusted manually using the sequence editor Se-Al (Rambaut, 2002). All sequences newly generated during this study were submitted to GenBank (Appendix) and the datasets and representative trees are deposited in TreeBASE (SN3872-20144).

Since they belong to a single non-recombining chloroplast genome, the *ndhF* and *trnLF* sequences were combined into a single dataset for analysis. The entire region of *ndhF* sequenced for the study (Olmstead & Sweere, 1994) was included in the analyses. However, a series of repeats and repeat fragments beginning ten nucleotides before the junction of the spacer and *trnF* gene and continuing into the *trnF* gene precluded unambiguous alignment of the 3' terminal portion of the *trnLF* region and, thus, was excluded. These repeats are similar to those reported by others (Vijverberg & Bachmann, 1999; Koch & al., 2005). Alignment gaps that were present in two or more of the ingroup taxa were coded as binary characters (Graham & al., 2000; Simmons & Ochoterena, 2000). Gaps that were informative only among outgroups were not scored.

Parsimony analyses utilized PAUP* vers. 4.0b10 (Swofford, 2002) with 200 initial replicates, random-order-entry starting trees, and TBR branch swapping with MULTREES and five trees saved per replicate. All transformations were equally weighted. A second round of analysis was then done using 1,000 starting trees and keeping only two trees per replicate, while using the strict consensus tree obtained from the first analysis as an inverse constraint to filter out trees compatible with that tree, thereby obviating the need to find all most-parsimonious

trees (Catalán & al., 1997). This procedure can be iterated, if necessary, until no further trees are discovered. No additional trees at the same or shorter lengths were obtained. Bootstrap analyses were conducted using 1,000 bootstrap replicates using TBR branch swapping, but with MULTREES off (DeBry & Olmstead, 2000).

RESULTS

The length of the portion of the *ndhF* sequence used in this study is 2,086 nucleotides in *Nicotiana tabacum*, whereas the total aligned length (including gaps to accommodate insertions and repeats) used in this analysis is 2,185 nucleotides. All gaps are even multiples of three and range in size from insertions and deletions of three nucleotides to a deletion of 48 nucleotides (in *Hyoscyamus albus*). The length of the *trnLF* sequence region in tobacco is 954 nucleotides. Unlike the *ndhF* sequences, which are entirely within the coding region of the gene, the *trnLF* sequences include mostly non-coding intron and spacer sequence. As a consequence, gaps are more frequent and variable in length. Most taxa in the Solanoideae have a region near the end of the *trnLF* spacer that is hypervariable for a series of long repeats, which often contain smaller insertions, deletions, and substitutions. An unambiguous alignment could not be obtained for this region, so it was not included in the analyses, leaving a total aligned length of 1,639 nucleotides. The combined length of the two regions, excluding the ambiguous portion of the *trnLF* spacer was 3,885 nucleotides.

The combined sequence dataset had a total of 1,138 parsimony informative nucleotide characters (769 in *ndhF*; 369 in *trnLF*), which, together with 80 coded gap characters (7 in *ndhF*; 73 in *trnLF*), yields a total of 1,218 characters in the analysis. Parsimony analysis of these data yielded numerous equally most-parsimonious trees (length = 4,720; CI = 0.56; RI = 0.79). The strict consensus tree with bootstrap values and one of the most parsimonious trees with branch lengths proportional to the inferred changes are shown in Figs. 1 and 2 respectively.

The strict consensus tree shows a high level of resolution with moderate to strong bootstrap support (ca. >70%) throughout the tree. Most of the unresolved nodes on the tree fall in terminal branches comprised of closely related species (e.g., within *Solanum*, *Capsicum*, *Lycium*, *Nicotiana*, etc.), but a few significant unresolved nodes remain among the main branches.

The genera *Duckeodendron*, *Sclerophylax*, *Nolana*, and the Antillean endemic genera *Goetzea*, *Espadaea*, *Henoonia*, and *Coeloneurum*, recognized as the separate families Duckeodendraceae, Sclerophylacaceae, Nolanaeae, and Goetzeaceae, respectively, are nested within the Solanaceae.

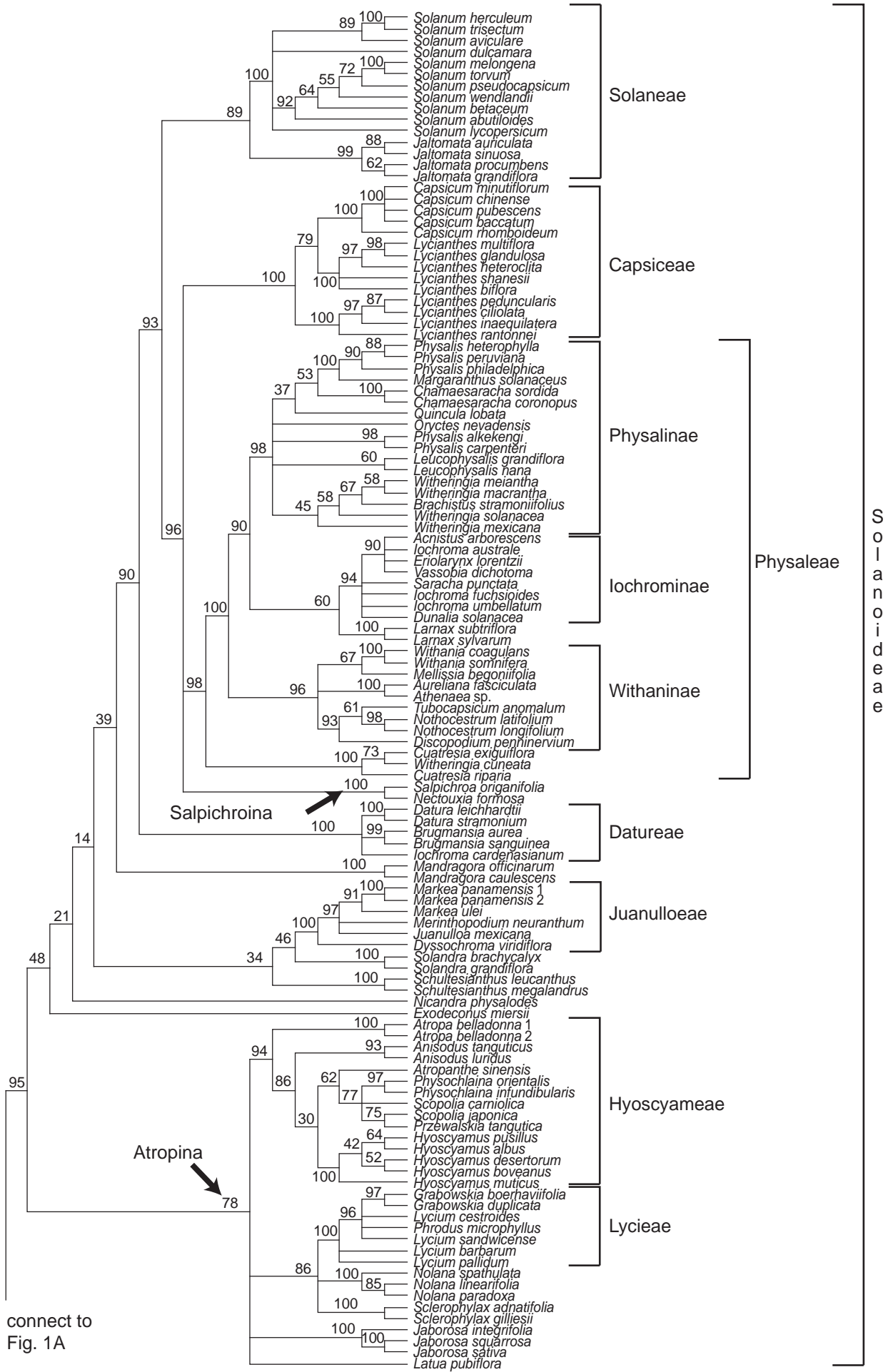
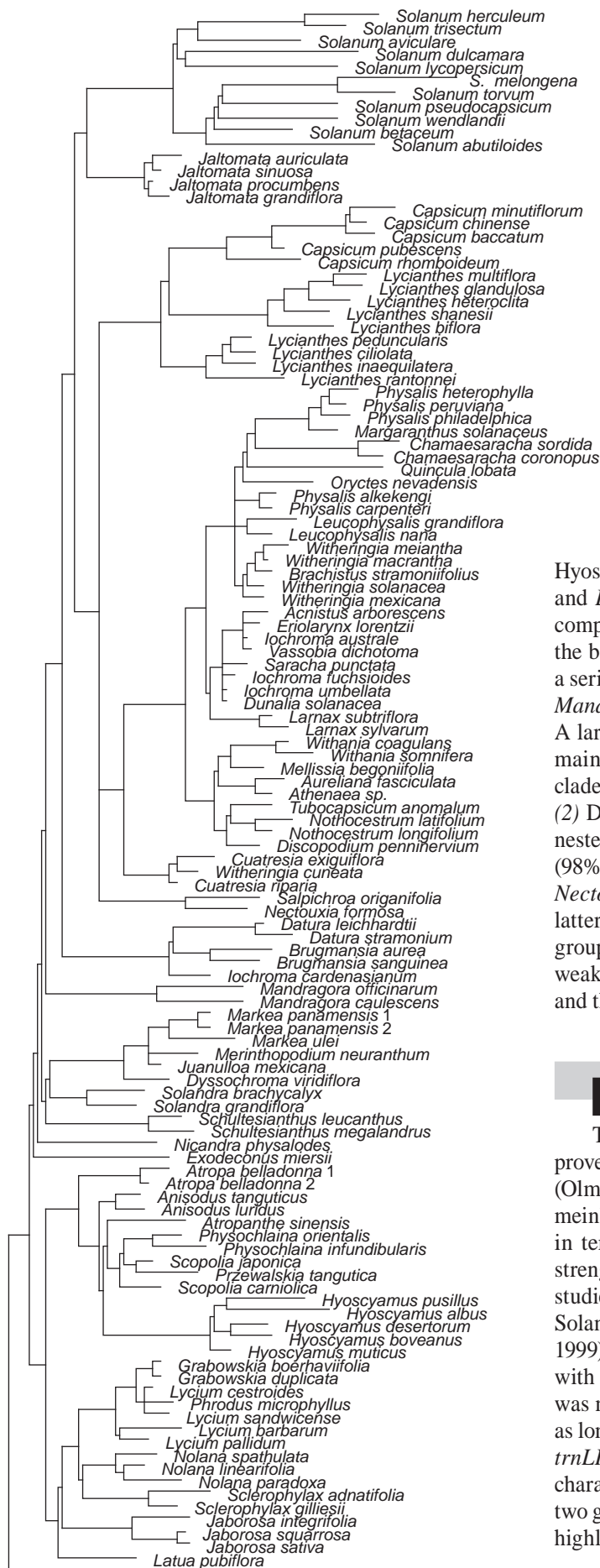




Fig. 2. Solanaceae phylogeny depicted as one of many equally most-parsimonious trees with inferred branch lengths (DELTRAN optimization in PAUP*) based on combined *ndhF* and *trnLF* sequences. Asterisk indicates this individual may be of hybrid origin (see text). Scale bar indicates ten inferred substitutions.



This analysis (Figs. 1–2) identifies *Schizanthus* as sister to the rest of the Solanaceae, with a clade comprising *Goetzea* and related genera plus *Metternichia* (Brazil) and *Tsoala* (Madagascar) as the next branch along with the monotypic Amazonian endemic *Duckeodendron* unresolved at this node. The next node on the tree includes four unresolved clades: (1) Cestroideae plus the Patagonian Benthamiellieae, (2) Petunieae, (3) Schwenckieae, and (4) the “ $x = 12$ ” clade. The “ $x = 12$ ” clade remains one of the most strongly supported major branches in the tree (99% BS) and is comprised of two strongly supported sister groups, Nicotianoideae (*Nicotiana* plus Anthocercideae; 99% BS) and Solanoideae (95%). Within the Solanoideae, a moderately well-supported clade (78%) comprising the Hyoscyameae, Lycieae, *Nolana*, *Jaborosa*, *Sclerophylax*, and *Latua* is sister to a weakly supported clade (48%) comprising the remainder of the Solanoideae. A grade at the base of the latter clade includes the Juanulloae and a series of genera of uncertain relationship (*Exodeconus*, *Mandragora*, *Nicandra*, *Solandra*, and *Schultesianthus*).

A large and species-rich clade makes up most of the remainder of the Solanoideae and contains four distinct clades: (1) Solaneae (*Jaltomata* plus *Solanum*; 89% BS), (2) Datureae (100% BS), (3) Capsiceae (with *Capsicum* nested within *Lycianthes*; 100% BS), and (4) Physaleae (98% BS). A small clade consisting of *Salpichroa* and *Nectouxia* belongs in an unresolved position with the latter two clades. The Physaleae comprise four distinct groups, subtribes Physalinae, Iochrominae (with *Larnax* weakly supported as sister to Iochrominae), Withaninae, and the genus *Cuatresia*.

DISCUSSION

The results of this analysis provide a significant improvement over past phylogenetic studies of Solanaceae (Olmstead & Palmer, 1992; Olmstead & al., 1999; Geimeinholzer & Wink, 2001; Martins & Barkman, 2005) in terms of taxonomic representation, resolution, and strength of support for many clades in the tree. In prior studies, *rbcL* provided relatively little information within Solanaceae (Olmstead & Sweere, 1994; Olmstead & al., 1999). Thus, for this study, *trnLF* was sequenced along with *ndhF*. Since *rbcL* was not available for most taxa, it was not included in analyses here. Though only ca. 45% as long as *ndhF*, the primarily noncoding sequence in the *trnLF* region has 60% as many parsimony informative characters as *ndhF*. Results of individual analyses of the two gene regions (not shown) were both well resolved and highly congruent with each other.

In general, results from past molecular phylogenetic studies are corroborated with additional support for many groups. In several cases, groups that were either poorly supported or ambiguous in resolution in past studies are now fully resolved and well supported. Results from the only molecular phylogeny based on nuclear DNA sequences with representative sampling throughout Solanaceae (Martins & Barkman, 2005) are consistent with these results in many places, as noted in the discussion of individual clades, but lack sufficient resolution or sampling to provide comparison with these results in many other places.

The results presented here confirm the inclusion of several genera often excluded from Solanaceae (e.g., *Goetzea* and related genera *Espadaea*, *Henoonia*, and *Coeloneurum*, *Nolana*, *Duckeodendron*, and *Sclerophyllax*) and extend those results to also include *Tsoala* within Solanaceae. Typically, justification for their exclusion in traditional classifications (e.g., Cronquist, 1981; Thorne, 1992; Takhtajan, 1997) was based on one or more traits, usually ovary and fruit characters, thought to be definitive for the group (see Hunziker, 2001), despite the recognition that the genera were closely related to Solanaceae. Knapp's treatment of fruit diversity in Solanaceae included this expanded view of gynoeceal morphology in the family (Knapp, 2002). The base of the tree includes a series of branches including *Schizanthus* and several taxa not traditionally assigned to Solanaceae, or controversial in their placement in Solanaceae: *Goetzea* and relatives, *Duckeodendron*, and *Tsoala*. The remaining taxa form a clade that is the core of the Solanaceae in all traditional treatments. Below we discuss important clades individually.

Schizanthus Ruiz & Pav. — This genus of twelve species is sister to the rest of the family. Many of its unusual traits, such as strongly bilateral floral symmetry, two fertile stamens, and resupinate flowers (Hunziker, 2001) are not found in other Solanaceae or their sister group, Convolvulaceae. Thus, they are most likely to be autapomorphies of an ancient lineage, rather than ancestral for the family. Within *Schizanthus*, phylogenetic analysis shows that the broad range of floral diversity is linked to pollinator diversity, with concerted evolution in floral traits associated with pollination syndromes proceeding from bee to hummingbird and moth pollination (Pérez & al., 2006). The restriction of *Schizanthus* to southern South America (Chile and Argentina) may reflect a southern hemisphere origin for the family (see below), but inferring ancestral states of either morphology or geographic ancestry from a relict sister group is inappropriate without solid phylogenetic information both above and below it on the tree. All reported counts indicate ten pairs of chromosomes. Ironically, Hunziker's (2001) classification recognizes the isolated nature of this genus by according it the rank of subfamily and citing molecular phylogenetic studies in

support of this (Olmstead & al., 1999), yet he placed it near the end of his schema in which taxa are ordered according to "their increasing complexity."

Goetzeoideae (Miers ex Airy Shaw) Thorne & Reveal. — The taxonomic placement of the small Antillean group consisting of *Goetzea*, *Espadaea*, *Henoonia*, and *Coeloneurum*, with a total of seven species, has been problematic due to differences in its fruit type (drupe), pollen, and wood anatomy relative to other putatively related families (Santiago-Valentin & Olmstead, 2003). After being assigned to several different families, they were first suggested to belong to Solanaceae by Wettstein (1895), but have most often been placed in their own family, Goetzeaceae, in recent classifications (Cronquist, 1981; D'Arcy, 1991; Thorne, 1992; Takhtajan, 1997; Hunziker, 2001). Olmstead & al. (1999) provided the first molecular evidence for their placement in Solanaceae. Subsequent studies (Fay & al., 1998; Santiago-Valentin & Olmstead, 2003) showed that the monotypic *Metternichia*, formerly placed near *Cestrum*, is related to *Goetzea*. In this study we find that the enigmatic and monotypic *Tsoala* also belongs here, as sister to *Metternichia* (tissue of *Tsoala* kindly provided by T. Derooin). *Tsoala* was placed initially in Solanaceae tribe Cestreae primarily due to similarities in pollen morphology with *Metternichia*, which was then assigned to Cestreae (Bossler & al., 1992). Hunziker (2001) disagreed with this placement, choosing instead to emphasize differences between the two genera. He also argued that the apparent lack of internal phloem in *Tsoala* excluded it from Solanaceae. However, tricolpate pollen with echinate exine sculpturing and a perforate tectum now can be seen to provide a potential synapomorphy for the clade of *Metternichia*, *Tsoala*, and the *Goetzea* group (Gentry, 1986; Bossler & al., 1992; Santiago-Valentin & Olmstead, 2003). *Tsoala* and *Metternichia* share the plesiomorphic trait for the family of capsular fruits, whereas members of the *Goetzea* group have drupes. *Metternichia* is from the coastal forests of southeastern Brazil and *Tsoala* is a monotypic Malagasy endemic genus once thought to be extinct (Bossler & al., 1992), but rediscovered in 2004 (G. Schatz, pers. comm.). Although the subfamily Goetzeoideae originally included just the Antillean genera (Olmstead & al., 1999), these results expand its circumscription to include *Metternichia* and *Tsoala*. Chromosome counts are available for *Espadaea* ($2n = 48$; Xiqués & al., 1994) and *Metternichia* ($2n = 26$; Moscone & al., 2005).

Duckeodendron Kuhlmann. — *Duckeodendron* is a monotypic genus of large trees native to lowland Amazonia. Hunziker (and others) excluded *Duckeodendron* from Solanaceae (Hunziker, 2001), primarily because of its drupaceous fruits, despite the fact that it does have internal phloem and floral characteristics consistent with Solanaceae. In our results, *Duckeodendron* is unresolved

with respect to Goetzeoideae and the rest of the Solanaceae exclusive of *Schizanthus*. Based on *rbcL* sequences, Fay & al. (1998) placed *Duckeodendron* sister to other Solanaceae to the exclusion of *Goetzea*, whereas Santiago-Valentin & Olmstead (2003) obtained a tree based on three chloroplast genes that united *Duckeodendron* with Goetzeoideae with modest support (78%). These two groups share a unique deletion in the *trnLF* spacer (scored as a character in the phylogeny analysis here), which may indicate monophyly of this group despite the fact that this relationship is not recovered in the present analysis. Unfortunately, inability to resolve this relationship prevents drawing conclusions about the origin of the drupe-like fruits shared by *Duckeodendron* and Goetzeoideae (Knapp, 2002). The chromosome number of *Duckeodendron* is unknown.

Benthamielleae Hunz. — This small group of three genera (*Benthamiella*, *Combera*, and *Pantacantha*) and 15 species from Patagonia and southern South America were assigned to the catch-all tribe Nicotinaeae in most traditional classifications (e.g., Hunziker, 1979). However, D'Arcy (1991) placed *Pantacantha* into Cestreae and Hunziker (2000) segregated these three genera of low shrub and mat-forming species into their own tribe Benthamielleae. These are sampled here for the first time in a molecular phylogeny and form a well-supported (100%) monophyletic group that is sister to Cestroideae, forming a clade with them with moderate support (73%). The three genera share a distinctive pollen morphology with large, irregularly shaped exine ornamentations (Stafford & Knapp, 2006). Chromosome counts indicate $x = 11$ for all three genera (Moscone, 1989). Whether they should be included in Cestroideae is a subjective decision, not contradicted by our results, but also not strongly supported by them.

Cestroideae Burnett. — Subfamily Cestroideae of traditional Solanaceae classifications (e.g., Hunziker, 1979; D'Arcy, 1991) forms a paraphyletic grade (Olmstead & Palmer, 1992; Olmstead & al. 1999) characterized by plesiomorphic traits in the family, including capsular fruits (Knapp, 2002) with small seeds containing straight embryos. Olmstead & al. (1999) suggested a much-reduced Cestroideae containing tribes Salpiglossideae Benth. sister to Browallieae Kostel. plus Cestreae Dumort. This is corroborated here with additional sampling, including the addition of *Sessea* in a position sister to *Cestrum* and *Protoschwenkia* as sister to Cestreae. Salpiglossideae once were treated as belonging to Scrophulariaceae (e.g., Bentham, 1846) due to their bilaterally symmetrical flowers, but they were recognized subsequently as members of Solanaceae (e.g., Wettstein, 1895). The traditional circumscription of tribes Cestreae and Salpiglossidae has fluctuated depending on the author, and D'Arcy (1978) combined the two tribes into Cestreae, in which he recognized 15 genera and about 500 species. Fourteen of these genera were sampled here, and only five of them (*Cestrum*, *Sessea*, *Browallia*,

Streptosolen, and *Salpiglossis*) emerge on our Cestroideae clade. That the traditional Salpiglossideae were not monophyletic was suggested by D'Arcy (1978) and confirmed by Olmstead & Palmer (1992). The most recent treatment (Hunziker, 2001) restricts the group to *Salpiglossis* and *Reyesia* (not sampled here), which together comprise six species from Chile and Argentina. *Salpiglossis sinuata*, the only species of the two genera included in the present analysis, is sister to the rest of Cestroideae (91%). Hunziker (1995, 2001) erected the tribe Browallieae to include *Browallia*, a group of about three to six species of annual herbs distributed from Arizona to Mexico and Bolivia and the monotypic shrub, *Streptosolen jamesonii* of Peru and Ecuador. Their pollen exhibit the unusual characteristics of having 5–8 colpi and a coarsely striated exine (Gentry, 1979; Stafford & Knapp, 2006). The molecular analysis confirms this view, uniting *Browallia* and *Streptosolen* in a well-supported clade (100%). *Protoschwenkia* was placed formerly in tribe Schwenckieae (Hunziker, 2001) and its unexpected placement in Cestroideae as sister to Cestreae (78%) was confirmed by sampling two separate accessions of this species (Appendix). The dorsifixed anther attachment in *Protoschwenkia* is inconsistent with other members of Schwenckieae and is similar to *Sessea* and other Cestroideae (Hunziker, 2001). The monotypic *Protoschwenkia* occurs in Andean Bolivia and adjacent Brazil, which also is consistent with the south temperate and Andean distribution of most Cestreae as opposed to the distribution of Schwenckieae in the more tropical regions of eastern South America and the Caribbean.

Tribe Cestreae consists of the small genera *Vestia* (one species from Chile) and *Sessea* (five Andean species) as successive sister groups to *Cestrum*. *Metternichia*, assigned to Cestreae in most treatments, is here placed in Goetzeoideae. *Vestia* and *Sessea* exhibit the capsular fruits characteristic of the rest of Cestroideae (and most other basal lineages of Solanaceae), whereas *Cestrum* has fleshy, berry-like fruits (Knapp, 2002). These three genera also lack the *Arabidopsis*-type telomeres typical of most angiosperms and found in all other Solanaceae examined (Sykorova & al., 2003). *Cestrum* represents a significant radiation relative to the rest of this clade, with about 175 species distributed throughout the tropical regions of the New World. The early diverging lineages of Cestroideae retain a southern Andean distribution and if, as seems likely, Benthamielleae are sister to this lineage, an origin in southern South America can be inferred. Chromosome counts for *Salpiglossis*, *Browallia*, and *Streptosolen* are predominantly $x = 11$ (with 10 and 12 reported in *Browallia* and *Streptosolen*, respectively). *Vestia* and *Cestrum* are $x = 8$. Counts are not available for *Protoschwenkia* and *Sessea*.

Petunieae Horan. — This clade includes an assemblage of genera assigned to various tribes (e.g., Nicotianeae, Salpiglossideae) in traditional classifications.

Petunia s.l. and *Fabiana* are sister to the remaining genera of this clade. Wijsman (1990) split *Petunia*, resurrecting the genus *Calibrachoa*. This split is consistent with chromosome base numbers of $x = 9$ for *Petunia* (also for *Fabiana*) and $x = 7$ for *Calibrachoa*. A cpDNA RFLP analysis (Ando & al., 2005) and DNA sequence analysis including both cpDNA and mtDNA (Kulcheski & al., 2006) confirm the monophyly of *Calibrachoa* and *Petunia*. However, *Fabiana* was not included in those studies. Our results suggest that *Fabiana* may be sister to *Calibrachoa*, but support is weak (68%) and sampling inadequate to lend confidence to that inference. Current work on *Fabiana* should resolve its relationship to *Petunia* and *Calibrachoa* (I. Peralta, pers. comm.) These taxa are distributed in southern South America with one species of *Calibrachoa* (*C. parviflora*) exhibiting a disjunct distribution between southern South America and North America.

Brunfelsia, with ca. 45 species, is widely distributed in tropical regions of South and Central America and has radiated in the Greater Antilles, with about 22 species found there. *Leptoglossis* and *Nierembergia* are South American, distributed principally from Peru to Argentina (with one species of the latter in Mexico), whereas *Bouchetia*, *Hunzikeria* and *Plowmania* are distributed from Guatemala and Mexico to the SW United States (with one species of the former in South America). Petunioideae seem likely to have originated in southern South America, where *Petunia*, *Calibrachoa*, *Fabiana*, *Leptoglossis*, *Nierembergia* and most of the potential sister groups (i.e., Cestroideae, Benthamiellieae, Schwenckieae, “ $x = 12$ ” clade) are located, and to have diversified northward into Central and North America in two lineages, *Brunfelsia* and the *Bouchetia*, *Hunzikeria*, *Plowmania* clade. Chromosome numbers based on $x = 11$ (*Brunfelsia*), 10 (*Leptoglossis*), 9 (*Petunia*, *Fabiana*, *Nierembergia*), 8 (*Bouchetia*, *Hunzikeria*, *Nierembergia*), and 7 (*Calibrachoa*) are all present in Petunioideae and appears to represent a descending aneuploid series in each of the two main branches of Petunioideae.

Schwenckieae Hunz. — This small clade of three genera and approximately 30 species is widely distributed in low elevation, tropical regions from the Antilles to Argentina. *Schwenckia* (ca. 25 spp.) and *Melananthus* (5 spp.) are both distributed throughout that range and the monotypic *Heteranthia* is a rare Brazilian endemic. Unusual corolla lobes with “lobules” flanking the lobes themselves, and two fertile stamens with ventrifixed anthers are distinguishing characters for the group (D’Arcy & Benitez de Rojas, 1991; Hunziker, 2001). Our results place the monotypic *Protoschwenckia* (endemic to the Andes), which lacks the corolla lobules and has dorsifixed anthers, with Cestroideae (see above), where it is a better fit geographically. Some earlier studies suggested that Schwenckieae may be the sister group to the rest of the family, although always with low bootstrap support (Fig. 1 in Olmstead &

al., 1999; Santiago-Valentin & Olmstead, 2003). The exact placement of Schwenckieae is uncertain in this study, but *Schizanthus* has moderate support as the first branch in Solanaceae, with Goetzeoideae and *Duckeodendron* both diverging before Schwenckieae. Chromosome counts of $n = 10$ and 12 have been reported for *Schwenckia* (Rao & D’Arcy, 1989; Chiarini, 2003). The widespread distribution of this small clade combined with the lack of resolution with respect to outgroups makes it difficult to speculate as to the geographic origin of this group.

“ $x = 12$ ” clade. — These results corroborate prior cpDNA (e.g., Olmstead & al., 1999) and nuclear *SAMT* (Martins & Barkman, 2005) studies in finding strong support (99%) for a clade that includes the traditional subfamily Solanoideae plus *Nicotiana* and the Australian endemic tribe Anthocercideae. Whereas Anthocercideae have been difficult to place to subfamily in previous classifications (Haegi, 1979, 1986), *Nicotiana* has never been placed with Solanoideae. This clade, with its putative cytological synapomorphy of chromosome numbers based on 12 pairs, was first recognized by Olmstead & Palmer (1992) and the informal name “ $x = 12$ ” clade given to it (Olmstead & Sweere, 1994).

Nicotianoideae Miers. — Most recent Solanaceae classifications have assigned *Nicotiana* to the tribe Nicotianeae (Hunziker, 1979, 2001; D’Arcy, 1991), which was a catch-all group containing *Nicotiana* and other genera lacking the defining traits of the other tribes of traditional Cestroideae (Anthocercideae, Cestreae, Salpiglossideae, Schwenckieae). In our results the other genera are distributed among Benthamiellieae and Petunioideae. *Nicotiana* is monophyletic and part of a larger well-supported clade that includes the Anthocercideae.

Anthocercideae G. Don. — Anthocercideae is an Australian clade (one species reaches New Caledonia) of seven genera and 31 species and is characterized by a suite of traits including flowers with a non-acrescent calyx, broadly actinomorphic corollas, and stamens with extrorse anther dehiscence attached low in the corolla tube (for more details, see Haegi, 1986; Garcia & Olmstead, 2003). Its relationship to other Solanaceae was unclear before molecular systematic studies placed it firmly with *Nicotiana* (Olmstead & Palmer 1992; Garcia & Olmstead 2003; Clarkson & al., 2004). Our results do not resolve Anthocercideae as monophyletic, with *Symonanthus* in an unresolved position relative to *Nicotiana* and the other six genera of Anthocercideae. However, Clarkson & al. (2004) provide evidence from more DNA regions to support monophyly of Anthocercideae and Garcia & Olmstead (2003) argue that the distinctive morphology shared by all seven genera support their monophyly. Our analysis includes one additional species of *Duboisia* (*D. hopwoodii*) and finds, as did previous studies, that our accession of *Cyphanthera albicans* is nested within *Duboisia*. In

a monograph of Anthocercideae, Haegi (1983) reports cases of natural hybridization between *D. myoporoides* and *C. albicans*. Material of *C. albicans* for our study was collected in a region of overlap in the distribution of these two species (B. Lepschi, pers. comm.) and may represent a hybrid individual with *D. myoporoides* as the maternal parent, hence the close sequence similarity in cpDNA between the two accessions in our study and previous studies that included these accessions (Garcia & Olmstead, 2003; Clarkson & al., 2004).

Nicotiana L. originated and diversified initially in the New World (ca. 50 species) and underwent a subsequent secondary radiation in Australia (section *Suaveolentes*, ca. 25 species) including one species in Africa (Olmstead & Palmer, 1991; Clarkson & al. 2004). Knapp & al. (2004) presented a revised sectional classification for *Nicotiana* based on recent molecular phylogenetic studies (Aoki & Ito, 2000; Chase & al. 2003; Clarkson & al., 2004).

Given that all of the probable outgroups to Nicotianoideae are New World in origin, it seems likely that the group originated in the New World. The basal split between Anthocercideae and *Nicotiana* means that the New World ancestor of Anthocercideae did not leave an extant lineage in the New World. Since the colonization of Australia by *Nicotiana* came relatively late in the diversification of that group, there must have been two dispersals to Australia in the history of Nicotianoideae to account for their present distribution. Thus, the common distribution in Australia of *Nicotiana* sect. *Suaveolentes* and Anthocercideae is coincidence, rather than further evidence of relationship.

Solanoideae Kostel. — The Solanoideae in its traditional circumscription (e.g., Hunziker, 1979; D'Arcy, 1991; but not Hunziker, 2001) is monophyletic (95%) and characterized by fleshy fruits (Knapp, 2002) with flattened seeds containing curved embryos, all of which represent derived traits in Solanaceae. Solanoideae have been recognized in virtually all prior classifications of Solanaceae, although Hunziker (2001) segregated Juanulloae into its own subfamily and continued the traditional practice of excluding *Nolana* and *Sclerophylax* from the family altogether. The SAMT study of Martins & Barkman (2005) also identified Solanoideae with strong support.

The base of this clade is well resolved in the strict consensus tree (Fig. 1), but with a series of branches having poor bootstrap support. Several small genera (*Exodeconus*, *Mandragora*, *Nicandra*, *Schultesianthus*, *Solandra*) represent lineages from the early diversification of this clade with no close relatives. Their phylogenetic isolation is reflected in traditional classifications in several instances where monogeneric tribes have been recognized (e.g., Mandragoreae, Nicandreae, Solandreae). Relationships suggested for some of these taxa in previous phylogenetic studies with limited sampling or data (e.g., *Exodeconus*

with *Nicandra*; Olmstead & Palmer, 1992; Olmstead & al., 1999; *Mandragora* with Hyoscyameae; Hoare & Knapp, 1997) are not corroborated here, although there continues to be weak support (46%) for *Solandra* with Juanulloae (Knapp & al., 1997; Olmstead & al. 1999).

Despite the weak support for the branching order at the base of Solanoideae, our results provide strong evidence of relationships among some groups that were not clear before. Apart from the isolated genera just mentioned, four clades, all with bootstrap support $\geq 78\%$, comprise the rest of Solanoideae: (1) Atropina (Hyoscyameae, Lycieae, *Jaborosa*, *Latua*, *Nolana*, and *Sclerophylax*), (2) Juanulloae, (3) Solaneae, Capsiceae, Physaleae, and Datureae, and (4) Salpichroina (*Salpichroa* and *Nectouxia*). The suffix “-ina” (Atropina and Salpichroina) is used here to denote unranked informal clade names (see Kron, 1997).

Atropina (Hyoscyameae Endl., Lycieae Lowe, Jaborosa Juss., Latua Phil., Nolana L., and Sclerophylax Miers). — Hyoscyameae is an Old World group comprising seven to eight genera and ca. 40 species (An-Ming & Zhang, 1986; D'Arcy & Zhang, 1992) and strongly supported as monophyletic in our analysis (94%). The characteristic circumscissile capsule, found in all species except *Atropa*, develops from a berry-like immature fruit, thus its ontogeny reflects its ancestry (Knapp, 2002). *Atropa* is sister to the rest of the Hyoscyameae in our analysis, as has been found in previous molecular phylogenetic studies (Olmstead & al. 1999; Yuan & al., 2006), but this relationship is not reflected in traditional classifications, where the berry-like fruit of *Atropa* typically results in its placement apart from other Hyoscyameae. On the basis of secondary chemistry, Tétényi (1987) placed *Atropa* with Hyoscyameae and *Mandragora*. The number of species in *Atropa* is controversial, with estimates of two (Hunziker, 2001), three (Hoare & Knapp, 1997), or five (D'Arcy, 1991). A second accession of *Atropa belladonna* was included here to confirm the placement of *Atropa* (Appendix). These results corroborate previous studies (e.g., Olmstead & al., 1999) that exclude *Mandragora* from this clade. Within Hyoscyameae, *Anisodus*, *Hyoscyamus*, and *Physochlaina* are found to be monophyletic, whereas *Scopolia*, with two widely disjunct species in Japan and Europe, is inferred to be paraphyletic with respect to the monotypic *Przewalskia* from the Tibetan plateau. *Physochlaina*, *Przewalskia*, and *Scopolia* form a clade (77%), which is corroborated by analysis of waxy gene sequences (Yuan & al., 2006).

Lycium is one of the largest genera of Solanaceae, with about 80 species distributed worldwide. It comprises the core of tribe Lycieae along with two small genera, *Grabowskia* (3–4 species mostly of southern South America, but with one disjunct in South America and Mexico) and *Phrodus* (one species from Chile). Morphological and molecular phylogenetic studies have shown

that *Grabowskia* is nested within *Lycium* (Bernardello & Chiang-Cabrera, 1998; Miller & Venable, 2000; Miller, 2002; Levin & Miller, 2005; Levin & al., 2007), a result that is corroborated here, with the additional conclusion that *Phrodus* also is derived from within *Lycium* (this is unresolved in Levin & Miller, 2005). If these results hold up, maintaining *Grabowskia* and *Phrodus* as distinct genera in a phylogenetic classification will be untenable and tribe Lycieae will be redundant with *Lycium*. However, evidence from the nuclear gene *waxy* places *Phrodus* as sister to *Lycium* and *Grabowskia*, albeit with weak support (Levin & al., 2007). Despite weak conflicting evidence from ITS (Miller & Venable, 2000; Miller, 2002), prior molecular phylogenetic studies of *Lycium* (Fukuda & al., 2001; Levin & Miller, 2005; Levin & al., 2007) concluded that there was a single colonization event in Africa with subsequent migration to Eurasia and Australia. All studies support a North American ancestry of the Hawaiian and Pacific Island species, *L. sandwicense* (as *L. carolinianum* var. *sandwicense* in Levin & al., 2007).

In addition to Hyoscyameae and Lycieae, the Atropina clade contains four genera mostly of temperate South America and extending up the Pacific coastal foothills of the Andes to Peru. Both *Nolana* and *Sclerophylax* are frequently segregated from Solanaceae and considered distinct families (e.g., Hunziker, 2001). *Nolana* has a curious fruit comprised of five or more carpels in which individual ovules intrude into the ovary wall forming distinct chambers and, ultimately a series of single-seeded mericarps (Bondeson, 1986). *Sclerophylax* also has fruit morphology atypical for Solanaceae, with ovules reduced to one or a few per carpel and forming a dry indehiscent fruit. *Nolana* comprises ca. 90 species distributed primarily in the coastal “lomas” formations in southern Peru and Chile (Tago-Nakazawa & Dillon, 1999; Dillon & al., 2007). *Sclerophylax* is mainly Argentine in distribution. *Jaborosa* (including *Trechonaetes*, represented here by *J. sativa*) is a genus of ca. 25 species in southern South America, primarily Argentina. *Latua* is a monotypic genus from Chile most commonly assigned to Nicotianeae (Hunziker, 1979; D’Arcy, 1991), or to its own tribe, Latueae (Hunziker, 2001) in the paraphyletic Cestroideae, which is consistent with its chromosome number of $n = 9$ (based on a single count in Plowman & al., 1971). The presence of a berry-like fruit in *Latua* dictated its placement in Solanoideae in early treatments (e.g., Bentham, 1876). Tétényi (1987) suggested a placement near *Jaborosa* based on embryological and secondary chemical traits, but this was disputed by Hunziker (2001). Because the molecular results reported here are at odds with the placement of the genus in recent classifications, we sampled two accessions of *Latua* to confirm our findings (Appendix).

The geographic distribution of Atropina suggests a history very similar to that of Nicotianoideae. Based on

outgroup distributions, an origin in the New World must be inferred, but, as was the case with Anthocercideae, no remnant lineage of Hyoscyameae is found there, and, as in *Nicotiana*, a relatively recent colonization event in *Lycium*, apparently to Africa, has led to its present distribution (Fukuda & al., 2001).

Juanulloae Hunz. — This clade of approximately five genera and 30 species is widely distributed in tropical regions of Central and South America, but is poorly known and generic boundaries are not clear (Knapp & al., 1997; but see Hunziker, 2001 for different generic circumscriptions). Many species are epiphytes or lianas, life forms unusual elsewhere in Solanaceae. Some genera are bat-pollinated and several are myrmecophilous. *Schultesianthus* usually is included in this group (Knapp & al., 1997; Hunziker, 2001), but here is only weakly supported (34%) in a clade along with Juanulloae and *Solandra*. The species of *Markea* sampled here (*M. panamensis* and *M. ulei*) were segregated into *Hawkesiophyton* by Hunziker (1977), but we follow terminology of Knapp & al. (1997) in this study. Thus *Markea* sensu Hunziker (2001) was not sampled. Morphological cladistic analyses (Persson & al., 1994; Knapp & al., 1997) suggested that *Schultesianthus* and *Solandra* were nested within Juanulloae, a relationship that is not supported here.

Solaneae, Capsiceae, Physaleae, Datoreae, Salpichroa Miers, and Nectouxia Kunth. — This clade was identified by Olmstead & al. (1999) in an analysis that focused on relationships within Solanoideae, but with very weak support. In our study, the clade has 90% bootstrap support and is further supported by the presence of a hypervariable region of the *trnLF* intergenic spacer consisting of long repeats and repeat fragments (not used in the analysis) that is not found elsewhere in the family. Similar repeats have been found in other groups (Asteraceae—Vijverberg & Bachmann, 1999; Brassicaceae—Koch & al., 2005). Within this clade, Datoreae is sister to a clade comprised of the other groups. The latter clade (93%) corresponds closely to tribe Solaneae sensu D’Arcy (1991) and Hunziker (2001) with the inclusion of *Nectouxia* and *Salpichroa* (assigned to tribe Jaborosae in those treatments).

Datoreae Dumort. — *Datura*, with eleven species, and *Brugmansia*, with ca. six species, are herbaceous and woody representatives of this group, respectively. These are among the most widely distributed and important hallucinogenic plants used by indigenous peoples in the New World (Schultes, 1979). Datoreae occupy a strongly supported position as sister to the large clade containing Solaneae, Capsiceae, Physaleae, and Salpichroina. Whether to retain *Brugmansia* as distinct from *Datura* is an old debate, but results of a cladistic analysis found both to be monophyletic and sister to each other (Persson & al., 1999), a result corroborated here, albeit with minimal sampling

(two species per genus). An unanticipated finding here is that *Iochroma cardenasianum* is found to belong in this clade (data kindly provided by S. Smith). *Iochroma cardenasianum* is a microphyllous shrub native to dry Andean environments in Bolivia. It has flowers very reminiscent of the “angel’s trumpet” flowers of *Brugmansia*, which may reach 30 cm or longer, but are much smaller, measuring about 3 cm in length. Despite early records of *Datura* in Asia and its presence in some interpretations of pre-Columbian texts from south Asia (Geeta & Gharaibeh, 2007), *Datureae* is probably a New World group that was transported to Asia early in post-European contact (Symon & Haegi, 1991; Daunay & al., 2007).

Salpichroina (*Salpichroa* Miers and *Nectouxia* Kunth). — *Salpichroa*, with ca. 15 species distributed primarily in Andean South America, and the monotypic *Nectouxia* of Mexico and west Texas form a well-supported clade of uncertain relationship to Capsiceae, Physaleae, and Solaneae. D’Arcy (1991) and Hunziker (2001) placed these genera with *Jaborosa* in tribe Jaboroseae based on the presence of trinucleate pollen, otherwise uncommon in the family. This apparently is a convergent trait.

Physaleae Miers. — Solaneae and Capsiceae are two of the most species-rich clades in Solanaceae, yet each has only two genera as presently conceived. In contrast, the closely related clade Physaleae has approximately 200 species divided into some 25 genera. Given that these clades are of comparable age (Capsiceae and Physaleae are sisters and Solaneae diverged shortly before, thus making it difficult to resolve relationships among them), it is curious why taxonomists have split Physaleae so finely at the rank of genus while in the other two clades few genera have been accepted. This may be due to the presence of the distinctive trait of poricidal anthers in *Lycianthes* and *Solanum*, thus leading to recognition of large clades as single genera in Capsiceae and Solaneae. Within Physaleae, we recognize five clades, Iochrominae, Physalinae, Withaninae, each with about eight genera, plus *Larnax* and *Cuatresia* as separate small clades. Hunziker (2001) recognizes four groups (subtribes within his Solaneae) comprising this set of taxa plus three genera (*Capsicum*, *Exodeconus*, *Jaltomata*) that do not belong with them in our analyses. Three of his groups each contain genera representing three or four of our clades, thus signifying a very different concept for his groupings. Before Hunziker’s most recent classification (Hunziker, 2001), most of the genera in Physaleae were assigned to a large tribe Solaneae in traditional classifications with no subdivisions indicating relationship (Wettstein, 1895; Hunziker, 1979; D’Arcy, 1991). Although our results do not permit strong inference on species-level relationships in Physaleae and, thus, conclusions about the monophyly of genera are not possible in most cases, relationships among the clades are well supported, with *Cuatresia* sister to the rest (Figs. 1B, 2B).

Cuatresia is a group of ca. eleven tropical lowland forest species distributed from Guatemala to Bolivia. It has often been confused with *Witheringia*, and Hunziker (2001) placed *Cuatresia* and *Witheringia* together with seven other genera in subtribe *Witheringinae*. However, *Witheringia* and *Cuatresia* are clearly distinct morphologically and phylogenetically. Several species originally described in *Witheringia* have been transferred to *Cuatresia*, and at least one other, *W. cuneata*, awaits transfer (Fig. 1).

Larnax and *Deprea* (not sampled here) are distributed primarily in the Andes from Colombia to Bolivia. Historically, the taxonomy of these genera has been confused, with species originally placed in seven genera now assigned to either *Deprea* or *Larnax* (Sawyer, 2005). Furthermore, the distinctions between the two genera have been unclear and have varied according to taxonomic opinion. Recent morphological cladistic work by Sawyer (2001, 2005) places seven species in *Deprea* and 25 in *Larnax*. The two genera can be distinguished by androecial and pollen characters as well as corolla shape (campanulate-rotate in *Larnax* vs. infundibular in *Deprea*). As a result of these studies, *Deprea sylvanum* was transferred to *Larnax*, and thus our sampling does not include species of *Deprea* as defined by Sawyer (2005). Our results place *Larnax* as sister to Iochrominae, but with weak support for the inclusive group (60%). Evidence from one morphological cladistic analysis suggested a placement for *Deprea* and *Larnax* near *Physalis*, in particular near the sometimes-segregated genus *Tzeltalia*, with which they share a woody habit and high elevation habitats (Estrada & Martinez, 1999), whereas another such study (Sawyer, 2005) suggested *Deprea* was close to *Witheringia* and *Larnax* was sister to most of Physaleae. However, nuclear ITS and *waxy* sequences do not place *Larnax* close to other Physaleae, but instead sister to Capsiceae (Whitson & Manos, 2005). A study using two nuclear gene regions (Smith & Baum, 2006) placed *Larnax* in Physaleae, but sister to *Cuatresia*. Obviously, more molecular work using intensive sampling within the Physaleae and Capsiceae is desirable to ascertain the phylogenetic relationships of *Deprea* and *Larnax*.

Withaninae Bohs & Olmstead, subtrib. nov.
Type genus: *Withania* Pauq. — Herbae frutices vel arbores pro parte maxima ex orbe antiquo. Flores in fasciculis axillaribus dispositi, pedunculis carentes. Corollae campanulatae urceolatae rotatae vel hypocrateriformes. Fila saepe appendicibus lateralibus conspicuis sulcum nectariferam formantibus. Comprendit genus *Withaniam* et genera propinqua.

Herbs, shrubs, or trees primarily from the Old World. Flowers in axillary fascicles; peduncle absent. Corollas campanulate, urceolate, rotate, or salverform. Filaments often with conspicuous lateral appendages forming nectar grooves. The subtribe includes *Withania* and related genera.

This small clade of ca. forty species is quite literally “all over the map”, with representatives in South America, Atlantic oceanic islands (e.g., Canaries, St. Helena), Africa, Europe, south, west, and east Asia, and the Hawaiian Islands. Few to no morphological synapomorphies have been identified for this clade, but all genera have axillary fasciculate inflorescences that lack peduncles. Many members of this clade have conspicuous lateral filament appendages that may form a “nectar groove”. However, other genera outside the clade may also exhibit these traits. Withanolide steroidal alkaloids are known from *Withania* and *Discopodium* (Hunziker, 2001), but these also occur in genera outside the clade (Tétényi, 1987).

Three small clades are identified in our results, with relationships among them unresolved. One clade includes *Athenaea* and *Aureliana* (100%) and is distributed in southern Brazil and adjoining regions of Argentina, Bolivia, and Paraguay. A second clade (67%) includes *Mellissia*, a monotypic genus from St. Helena, and *Withania*, the largest and most widely distributed genus in the group, occurring from the Canary Islands across Africa, southern Europe, and Asia. *Mellissia* was thought to be extinct before being rediscovered in the 1990's (Fay & al., 2007; previously unpublished *ndhF* sequence kindly provided by Q. Cronk). Debate over generic concepts for *Withania* (i.e., whether to include *Archiphysalis*, *Mellissia*, and *Physaliastrum*) has led to disagreement over the number of genera recognized (D'Arcy & Zhang, 1992; Hunziker, 2001). Hunziker (2001) included *Mellissia* within *Withania*, and the molecular results support their close relationship. Styly heteromorphism has been noted in *Athenaea*, *Aureliana*, and *Withania*, and several species of *Withania* have been shown to be dioecious (Hunziker, 2001; Anderson & al., 2006). Thus, heterostyly may be a morphological feature that unites the *Withania* and *Athenaea/Aureliana* clades. The third clade (93%) includes *Nothoestrum*, with four species endemic to Hawaii, *Tubocapsicum* (one species, China), and *Discopodium*, a monotypic genus from the mountains of equatorial Africa. Virtually all of the rest of Physaleae is New World in distribution, so the *Athenaea/Aureliana* clade probably represents a relict distribution from the common ancestor of Withaninae. The sister group relationship between *Tubocapsicum* and *Nothoestrum* and the fact that the most likely outgroups to this clade are from Africa or Eurasia suggests that the Hawaiian endemic *Nothoestrum* most likely arrived from the west. The remarkable geographic distribution in this small group is unrivaled in the family, except by *Lycium* and *Solanum*, each of which is a much larger group.

Iochrominae (Miers) Hunz. — This is a well-supported clade (94%) comprising *Acnistus*, *Dunalia*, *Eriolarynx*, *Iochroma*, *Saracha*, and *Vassobia*. Relationships within this clade are poorly resolved in our study. *Iochroma*, represented by three species here, does not

appear to be monophyletic. A detailed phylogenetic study of Iochrominae (Smith & Baum, 2006) produced greater resolution and found generic boundaries to be in disarray. A companion study of the evolution of flower size, shape, and color suggested that response to pollinator preference has led to convergence in traits traditionally used to define genera (Smith & Baum, 2007). Our study found weak support (60%) for *Larnax* as sister to Iochrominae; both groups are primarily Andean in distribution. However, they are a poor fit with Iochrominae morphologically and a clade comprising Iochrominae, *Deprea* and *Larnax* is not supported by nuclear gene data (Whitson & Manos, 2005; Smith & Baum, 2006). *Iochroma cardenasianum* from Bolivia falls out in Datureae, a result corroborated by a nuclear gene phylogeny (S. Smith, pers. comm.).

Physalinae (Miers) Hunz. — Physalinae is dominated by *Physalis*, with more than 75 species and a center of diversity in Mexico and North America. Morphological cladistic analyses (Axelius, 1996; Estrada & Martinez, 1999) suggest that *Margaranthus* and possibly *Chamaesaracha*, *Leucophysalis*, and *Quincula* are derived from within *Physalis*. In our results, the type and sole Asian species, *P. alkekengi*, falls out with the eastern North American *P. carpenteri* in a small clade separate from the other samples of *Physalis* (98%). A study of *Physalis* and related genera using nuclear DNA sequences (Whitson & Manos, 2005) was largely consistent with our results. They found a Central American clade consisting of *Witheringia* and *Brachistus*, with *Tzeltalia* and *Leucophysalis viscosa* (the latter two taxa not sampled here) sister to the rest of Physalinae, followed by a branch containing *P. alkekengi* and *P. carpenteri*. Their results are also consistent with ours in finding a clade comprised of *Witheringia* and *Brachistus*. Our study suggests that *Witheringia* is paraphyletic with respect to *Brachistus*. Despite the poor resolution at the base of Physalinae and the sparse sampling of *Physalis*, it appears that a clade comprising all *Physalis* species would also include at least *Chamaesaracha* and *Margaranthus* and possibly *Oryctes*, *Quincula*, and *Leucophysalis*, all of which occur in Central and North America (except *P. alkekengi*).

Capsiceae Dumort. — *Lycianthes* was first segregated from *Solanum* on the basis of a novel fruit morphology (Hassler, 1917, described in Hunziker, 2001). However, *Capsicum* and *Lycianthes*, which together comprise this clade, share a derived anatomical trait of ten nerves in the calyx vasculature as opposed to five in *Solanum* and most Solanaceae (D'Arcy, 1986a). Previous molecular phylogenetic studies have confirmed a close relationship between *Capsicum* and *Lycianthes* (Olmstead & Palmer, 1992; Bohs & Olmstead, 1997; Olmstead & al., 1999; Walsh & Hoot, 2001). Ironically, this fact has been used to support the segregation of *Lycianthes* from *Solanum*, but not to place it with *Capsicum* (Hunziker, 2001); instead,

the shared poricidal anthers of *Solanum* and *Lycianthes* were deemed more important in classification. For example, Hunziker (2001), citing D'Arcy's (1986a) work, said: "D'Arcy ... demonstrated undoubtedly that *Lycianthes* is more closely related to *Capsicum* than to *Solanum* ..." yet still placed *Lycianthes* with *Solanum* in his subtribe Solaninae and *Capsicum* with several other genera in subtribe Capsicinae. *Lycianthes* is one of the largest genera in Solanaceae with 150 to 250 species (Hunziker, 2001; Dean, 2004) and is distributed in the Neotropics and tropical SE Asia, whereas *Capsicum* has ca. 30 species and is restricted to the New World, where it is widely distributed from the southwestern U.S. to Argentina. Olmstead & al. (1999) suggested that *Capsicum* was derived from a paraphyletic *Lycianthes*, based on cpDNA restriction site data and a limited sampling of five species of *Lycianthes* and two of *Capsicum*. However, a study by Walsh & Hoot (2001) based on chloroplast *atpB-rbcL* spacer and nuclear *waxy* sequences found both genera to be monophyletic, though with weak bootstrap support for both clades. Our results find moderately strong support for a paraphyletic *Lycianthes*, with *Capsicum* and one clade of *Lycianthes* joined with 79% bootstrap support. Given that *Capsicum* is a Linnaean genus and *Lycianthes* was described much more recently, a taxonomic change to recognize this would require either that some or all of *Lycianthes* be transferred to *Capsicum*, or that *Lycianthes* be split into at least two genera. The type of *Lycianthes* is *L. lycioides* (L.) Hassler, which was not sequenced in this study, but has been included in previous molecular systematic analyses (Olmstead & al., 1999; Walsh & Hoot, 2001), where it is closely related to *L. rantonnei*; thus, at minimum, the clade sister to *Capsicum* would have to be renamed in order for genera in Capsiceae to be monophyletic.

Solanaceae Dumort. — *Solanum*, with ca. 1,400 species (D'Arcy, 1991; Nee, 1999; Hunziker, 2001; S. Knapp, pers. comm.) constitutes approximately half the species in Solanaceae. As such, it has been the focus of several molecular phylogenetic studies aimed at understanding the entire genus (Bohs & Olmstead, 1997, 1999; Olmstead & Palmer, 1997; Bohs, 2005; Weese & Bohs, 2007), or portions of it (e.g., Palmer & Zamir, 1982; Hosaka & al., 1984; Spooner & al., 1993; Bruneau & al., 1995; Castillo & Spooner, 1997; Bohs & Olmstead, 2001; Peralta & Spooner, 2001; Bohs, 2004, 2007; Spooner & al., 2004, 2005; Levin & al., 2005, 2006; Martine & al., 2006). These studies have shown that several segregate genera, including *Cyphomandra*, *Lycopersicon*, *Normania*, and *Triguera*, belong within *Solanum*. Perhaps equally important for understanding the evolution of the family, these studies have confirmed that *Lycianthes* does not belong with *Solanum*. Like *Solanum*, *Lycianthes* has anthers opening by terminal pores, a trait sufficiently distinctive to suggest a close relationship between the two. Prior molecular phylogenetic

studies have not been able to resolve the sister group to *Solanum* with confidence, with either *Jaltomata* or *Capsicum* plus *Lycianthes* suggested by different analyses (Olmstead & Palmer, 1992, 1997; Bohs & Olmstead, 1997; Olmstead & al. 1999). Resolution of this sister group to *Solanum* is important for understanding the evolution of poricidal anthers, because, if Capsiceae is the sister group to *Solanum* and *Capsicum* (without poricidal anthers) is derived from within *Lycianthes* (as seems to be the case; see above), then a single origin in the common ancestor of the inclusive group might account for the presence of this trait in both genera. However, our results find strong support (89%) for *Jaltomata* as sister to *Solanum* and likewise for Capsiceae to form a clade (96%) with Physaleae, *Salpichroa* and *Nectouxia*. Weese & Bohs (2007) also found strong support for *Jaltomata* as sister to *Solanum* based on a combined analysis of three nuclear and chloroplast genes. Thus, two origins of poricidal anthers is a more parsimonious explanation for the presence of this trait in these two groups.

Jaltomata is a genus of ca. 50 species distributed from the southwestern U.S. through Central America and the Andes to Bolivia, with a center of diversity in Peru. Phylogenetic analysis identified two primary lineages; one in South America and one in Mesoamerica (Mione & al., 1994). *Solanum* has a worldwide distribution, with centers of diversity in tropical America, Africa, and Australia. *Solanum* consists of about 12 to 15 major clades (Bohs, 2005; Weese & Bohs, 2007), the largest of which comprises subgenus *Leptostemonum*, the "spiny solanums" (Levin & al., 2006). The South American *S. thelopodium* group emerges as sister to the remainder of *Solanum* (Bohs, 2005; Weese & Bohs, 2007). This relationship, combined with the New World distribution of its sister genus *Jaltomata*, indicates that *Solanum* originated in the Americas, most likely in South America, and radiated several times to the Old World.

BIOGEOGRAPHY

A well-resolved phylogeny with reasonably comprehensive sampling, along with phylogenetic studies of the more inclusive group Solanales (Bremer & al. 2002; Stefanovic & al., 2002), also permits the exploration of biogeographic history of Solanaceae. The Solanales comprise two large sister clades, Solanaceae and Convolvulaceae, and five small genera, *Hydrolea*, *Grevea*, *Kaliphora*, *Montinia*, and *Sphenoclea* (Bremer & al., 2002; APG II, 2003). *Hydrolea* and *Sphenoclea* are sister taxa and comprise ca. twelve species distributed in tropical regions of the New and Old Worlds. The other three genera comprise Montiniaceae (Bremer & al., 2002) and are restricted to South Africa and Madagascar. Within Convolvulaceae, *Humbertia*,

a Malagasy endemic, is sister to the rest of the family, followed by two branches comprised of species from SE Asia and Madagascar (Stefanovic & al., 2002). New World taxa do not appear until higher in the tree, in the two main clades that form the core of Convolvulaceae. In light of the southern connections elsewhere at the base of Solanales, the placement of *Schizanthus* (southern South America) and Goetzeoideae (southern Brazil, Madagascar, and the Antilles) at the base of the Solanaceae suggests strongly that the Solanales are of southern hemisphere origin and possibly owe their early diversification to the break-up of Gondwana. If this is true, the distribution of *Tsoala* in Madagascar might be an ancient relict of that Gondwanan ancestor and be the only Old World relictual lineage in the Solanaceae. A poor fossil record for Solanaceae has thus far hampered establishment of the timing of origin of the Solanaceae. However, in an effort to estimate ages of major lineages of angiosperms (Wikstrom & al., 2001), a suggested minimum date of origin for the Solanales of 82–86 million years before present (bearing in mind a substantial error in any such estimates; Hillis & al., 1996; Magallon, 2004) suggests an origin of Solanaceae close in time to the split-up of Gondwana.

The relative completeness of the sampling and the resolution of our results permit an estimate of the number of lineages that have successfully colonized (without human assistance) outside of the New World (excluding *Solanum*). Lineages outside of the New World include: (1) *Tsoala*, (2) *Nicotiana* subgenus *Suaveolens*, (3) *Anthocercidae*, (4) one clade of *Lycium*, (5) *Hyoscyameae*, (6) *Mandragora*, (7) part of *Withaninae* (probably one event), (8) *Physalis alkekengi*, and (9) part of *Lycianthes* (the phylogeny of *Lycianthes* is still poorly known, but a relatively small group of about 20 species exists in SE Asia and may represent a single lineage). Thus, depending on whether *Tsoala* represents a relictual lineage or a colonization event, eight or nine dispersal events have led to successful diversification outside of the New World. Of course, if Solanaceae turns out to be much older than presently believed, then some other lineages could represent relictual Gondwanan lineages, but this seems unlikely to be the case. *Solanum* appears to represent a minimum of five additional events (Bohs, 2005; Levin & al., 2006; Weese & Bohs, 2007), although sufficient sampling is not yet available to permit more precise inference. The majority of Old World species in the large *Leptostemonum* clade (“spiny” solanums) appears to owe their distribution to a single colonization event (Olmstead & Palmer, 1997; Levin & al., 2006).

Three genera of Solanaceae have native species on Hawaii (*Lycium*, *Nothocestrum*, *Solanum*). The three endemic Hawaiian species of *Solanum* apparently belong to the Old World clade of *Leptostemonum* with connections to other South Pacific or Australasian species (Levin &

al., 2006; Whalen, 1984). Evidence from phylogenetic studies now suggests that colonization from the New World (*Lycium*), Asia (*Nothocestrum*), and the South Pacific (*Leptostemonum*) all contributed to the indigenous Hawaiian Solanaceae flora.

CHROMOSOME EVOLUTION

A traditional view of chromosomal evolution in Solanaceae posited a base chromosome number of $x = 12$ (Raven, 1975), which typifies nearly 85% of the species in the family. This was consistent with the traditional perception that Solanoideae represented the “generalized” or ancestral subfamily (e.g., D’Arcy, 1979). However, the inference from phylogeny implies that $x = 12$ is a derived condition in Solanaceae, where it characterizes the large $x = 12$ clade. Isolated counts of $x = 12$ have been reported in *Espadaea*, *Schwenckia*, and *Streptosolen* which do not belong to the $x = 12$ lineage (Hunziker, 2001). Outside the $x = 12$ clade, several chromosome base numbers are found, but all are lower than $x = 12$. The ancestral condition for Cestroideae and Benthamiellieae can be inferred to be $x = 11$. In Petunieae, reduction in chromosome base number is apparent in the branches leading to *Petunia* ($x = 7$) and to *Bouchetia* and *Hunzikeria* ($x = 8$), but the ancestral number is equivocal, with 9, 10, or 11 as possibilities. Limited counts for Goetzeoideae ($x = 12$ or 13) and Schwenckieae ($x = 10$ or 12) and the absence of any counts for *Duckeodendron* prevent any firm inference regarding ancestral base chromosome number in those clades. *Schizanthus*, which is sister to the rest of Solanaceae, is consistently $x = 10$. Critical information from Convolvulaceae, the sister group to Solanaceae, is missing for many early diverging branches, but $x = 9–15$ are reported elsewhere in the family (Raven, 1975; S. Stefanovic, pers. comm.). Base chromosome numbers elsewhere in Solanales (e.g., Montiniaceae, Sphenocleaceae, Hydroleaceae) include $x = 8, 10, \text{ and } 12$. Thus it seems difficult to speculate at this time on the ancestral chromosome number for Solanaceae.

CONCLUSIONS

These results provide a framework phylogeny for the entire family that can help integrate many previously published phylogenetic studies within Solanaceae. A comprehensive revision of the classification of Solanaceae is now within reach. However, several areas still require further study. Whereas sampling for this study was not intended to address monophyly of genera in the family, several genera appear to be non-monophyletic, including *Lycianthes* (e.g., with respect to *Capsicum*), *Physalis*

(e.g., *Chamaesaracha*, *Margaranthus*), *Browallia* (e.g., *Streptosolen*), *Cyphanthera* (e.g., *Crenidium*, *Duboisia*), and *Lycium* (e.g., *Grabowskia*, *Phrodus*). Resolution of relationships and generic limits are notably weak in each of the subtribes of Physaleae. Identification of the sister to the “ $x = 12$ ” clade still eludes us and the basal relationships among Solanoideae are poorly supported. A framework phylogeny such as this can also provide the basis for inference into the time of origin of major lineages of Solanaceae. However, this endeavor is hampered by the limited fossil evidence on which to base a calibration for a molecular clock. Nonetheless, this family-wide phylogeny provides an abundance of hypotheses for testing phylogenetic, ecological, evolutionary, and biogeographical questions both within the Solanaceae and in the broader context of the angiosperms.

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Appendix. Taxa and vouchers for species sampled.

Species, geographic origin (specific to collection, if known, otherwise general for species), collector and collection number (herbarium), *ndhF* GenBank accession no./*trnLF* GenBank accession no.

Acnistus arborescens (L.) Schldtl., Central and South America, Bohs 2577 (UT), EU580855/EU580954; *Anisodus luridus* Link, China, BIRM S.0215/71 (BIRM), EU580856/EU580955; *Anisodus tanguticus* (Maxim.) Pascher, Australia, Ho & al. 118 (GH), EU580857/EU580956; *Anthocercis angustifolia* F. Muell., Australia, Olmstead 94-05 (WTU), AY098704/AY098671; *Anthocercis gracilis* Benth., Australia, H. Stace s.n. (UWA), AY098705/AY098672; *Anthocercis ilicifolia* Hook., Australia, Stace s.n. (UWA), AY098706/AY098673; *Anthocercis intricata* F. Muell., Australia, Stace s.n. (KPBG), AY098707/AY098674; *Anthocercis littorea* Labill., Australia, H. Stace s.n. herb. uncertain (UWA), (PERTH), or (KPBG), AY098708/AY098675; *Anthocercis sylvicola* T.D. McFarl. & Ward.-Johnson, Australia, Middleton s.n. (PERTH), AY098709/AY098676; *Anthocercis viscosa* R. Br., Australia, Symon 14835 (AD), U08914/AY098677; *Anthotroche blackii* F. Muell., Australia, Stace s.n. (KPBG), AY098711/AY098678; *Anthotroche myoporoides* C.A. Gardner, Australia, Stace s.n. (KPBG), AY098810/AY098679; *Anthotroche pannosa* Endl., Australia, Stace s.n. (KPBG), AY098712/AY098680; *Anthotroche walcottii* F. Muell., Australia, Bellairs & Bellairs 2035 (PERTH), AY098713/AY098681; *Athenaea* sp., Brazil, D'Arcy (MO), EU580858/EU580957; *Atropa belladonna* L. 1, Eurasia, BIRM S.0078 (BIRM), U08915/-; *Atropa belladonna* L. 1, Eurasia, Olmstead s.n. (WTU), -/EU580958; *Atropa belladonna* L. 2, Eurasia, BIRM S.0051 (BIRM), EU580859/EU580959; *Atropanthe sinensis* (Hemsl.) Pascher, China, Schneider 2407 (GH), EU580860/EU580960; *Aureliana fasciculata* (Vell.) Sendtn., Brazil, Brown s.n. (IAC), EU580861/EU580961; *Benthamiella skottsbergii* A. Soriano, Argentina, Leuenberger & Arroyo 3711 (CORD), EU580862/-; *Boucheitia erecta* Dunal, Mexico, SW U.S.A., D'Arcy 1791 (MO), EU580863/EU580962; *Brachistum stramonifolium* (Kunth) Miers, Central America, Sousa-Pena 738a (CONN), EU580864/EU580963; *Browallia eludens* Van Devender & P.D. Jenkins, U.S.A., Jenkins & al. 90-106 (WTU), EU580865/EU580964; *Browallia speciosa* Hook., South America, BIRM S.0416 (BIRM), AY206739/AY206753; *Brugmansia aurea* Lagerh. = *Methysticodendron amesianum* R.E. Schult. or *B. amesianum* (R.E. Schult.) D'Arcy, Colombia, BIRM S.0412 (BIRM), EU580866/EU580965; *Brugmansia sanguinea* (Ruiz & Pav.) D. Don, Colombia, Olmstead s.n. (WTU), EU580867/EU580966; *Brunfelsia americana* L., Antilles, Matthaei Bot. Gard. #840215, no voucher, AY206740/AY206754; *Brunfelsia uniflora* (Pohl) D. Don, Brazil, Brown s.n. (UEC), EU580868/EU580967; *Calibrachoa parviflora* (Juss.) D'Arcy, U.S.A., Sanders 5835 (COLO), EU580869/EU580968; *Capsicum baccatum* L., Bolivia, Eshbaugh E1584 (MU), U08916/EU580969; *Capsicum chinense* Jacq., in cult., Bohs 3088 (UT), EU603442/EU603443; *Capsicum minutiflorum* (Rusby) Hunz., Bolivia, Bohs & al. 3012 (UT), DQ667543/EU580970; *Capsicum pubescens* Ruiz & Pav., in cult., Bohs 2565 (UT), DQ667544/-; *Capsicum rhomboideum* (Dunal) Kuntze, Ecuador, Heiser 7518 (IND), DQ667545/EU580971; *Cestrum macrophyllum* Vent., Puerto Rico, Olmstead 2003-10 (WTU), EU580870/EU580972; *Cestrum megalophyllum* Dunal, Bolivia, Bohs & Nee 2756 (UT), EU126005/EU580973; *Cestrum nocturnum* L., Central America, Northern South America, Olmstead s.n. (WTU), AY206741/AY206755 & AY206723; *Cestrum pittieri* Francey, Costa Rica, Bohs 2922 (UT), EU126006/EU580974; *Cestrum rigidum* Rusby, Bolivia, Nee & Bohs 49653 (NY), EU126007/EU580975; *Cestrum strigilatum* Ruiz & Pav., Bolivia, Bohs & Nee 2811 (UT), EU126008/EU580976; *Cestrum tomentosum* L. f., Costa Rica, Bohs 2933 (UT), EU126009/EU580977; *Chamaesaracha coronopus* (Dunal) A. Gray, U.S.A., Turner 15854 (TEX), EU580871/EU580978; *Chamaesaracha sordida* (Dunal) A. Gray, U.S.A., Olmstead 92-245 (WTU), EU580872/EU580979; *Coeloneurum ferrugineum* Urb., Dominican Republic, Santiago 93-201 (MAPR), AY206742/AY206756 & AY206724; *Combera paradoxa* Sandwith, Argentina, Bernadello & Moscone 658 (CORD), EU580873/EU580980; *Crenidium spinescens* Haegi, Australia, Lepschi & Lally 1672 (CANB), AY098714/AY098682; *Cuatresia exiguiflora* (D'Arcy) Hunz., Costa Rica, Bohs 2454 (UT), EU126010/EU580981; *Cuatresia riparia* (Kunth) Hunz., Costa Rica, Bohs 2551 (UT), EU126011/EU580982; *Cyphanthera albicans* Miers, Australia, Lepschi & Lally 1732 (CANB), AY098715/AY098683; *Cyphanthera anthocercidea* Haegi, Australia, Haegi 1456 (AD), AY098716/AY098684; *Cyphanthera microphylla* Miers, Australia, Lepschi 2170 (PERTH), AY098717/AY098685; *Cyphanthera odgersii* (F. Muell.) Haegi, Australia, Chinnock 3100 (AD), AY098718/AY098687; *Datura leichhardtii* Benth., Australia, D'Arcy 17759 (MO),

Appendix. Continued.

EU580874/EU580983; *Datura stramonium* L., U.S.A., *Olmstead s.n.* (WTU), U08917/EU580984; *Discopodium penninervium* Hochst., Uganda, *Knapp* 9808 (BM), EU126012/EU580986; *Duboisia hopwoodii* (F. Muell.) F. Muell., Australia, *Lepschi & al.* 4438 (CANB), EU580876/EU580987; *Duboisia leichhardtii* (F. Muell.) F. Muell., Australia, *Haegi* 2056 (AD), AY098719/AY098689; *Duboisia myoporoides* R. Br., Australia, *Symon* 14832 (AD), AY098720/AY098690; *Duckeodendron cestroides* Kuhl., Brazil, *Ribeiro* 1189 (K), AY206743/AY206757 & AY206725; *Dunalia solanacea* Kunth, Ecuador, *Smith* 211 (WIS), EU580877/EU580988; *Dysochroma viridiflora* Miers, Brazil, *Brown s.n.* (IAC), EU580878/EU580989; *Eriolarynx lorentzii* (Dammer) Hunz., Argentina, *Olmstead S-18* (WTU), (BIRM S.0376), EU580879/EU580990; *Espadaea amoena* A. Rich., Cuba, *Santiago* 93-202 (UPR), AY206744/AY206758 & AY206726; *Exodeconus miersii* (Hook. f.) D'Arcy, Galapagos Is., BIRM S.1223/73 (BIRM), EU580880/EU580991; *Fabiana imbricata* Ruiz & Pav., Argentina, *Olmstead s.n.* (WTU), EU580881/EU580992; *Goetzea ekmanii* O.E. Schulz, Dominican Republic, *Santiago* 96-2a (WTU), AY206745/AY206759 & AY206727; *Goetzea elegans* Wydl., Puerto Rico, *Olmstead* 92-220 (WTU), AY206746/-; *Goetzea elegans* Wydl., Puerto Rico, *Santiago* 89-6 (MAPR, WTU), -/AY206760; *Grabowskia boerhaviifolia* (L. f.) Schltldl., Argentina, BIRM S.1801/76 (BIRM), EU580882/-; *Grabowskia boerhaviifolia* (L. f.) Schltldl., Argentina, *Bernardello* 894 (CORD), -/DQ124554; *Grabowskia duplicata* Arn., Argentina, BIRM S.0258/66 (BIRM), EU580883/-; *Grabowskia duplicata* Arn., Argentina, *Bernardello & Vesprini* 898 (CORD), -/DQ124555; *Grammosolen dixonii* (F. Muell. & R. Tate) Haegi, Australia, *Symon* 14833 (AD), *Olmstead s.n.* (WTU), AY098721/AY098691; *Grammosolen truncatus* (Ising) Haegi, Australia, *Canty* 2429 (AD), AY098722/AY098692; *Henoonia myrtifolia* Griseb., Cuba, *Santiago* 96-15 (WTU), AY206747/AY206761 & AY206728; *Hunzikeria texana* (Torr.) D'Arcy, U.S.A., *Ferguson* 089 (TEX), EU580886/EU580993; *Hyoscyamus albus* L., Mediterranean Europe, BIRM S.1218/81 (BIRM), EU580887/EU580994; *Hyoscyamus boveanus* Asch. & Schweinf., Egypt, *Abdel-Migid s.n.* (WTU), EU580888/EU580995; *Hyoscyamus desertorum* (Asch. & Boiss.) Tackholm, Afghanistan, Herb. of late E. India Co. #5924 (GH), EU580889/EU580996; *Hyoscyamus muticus* L., Egypt, *Abdel-Migid s.n.* (WTU), EU580890/EU580997; *Hyoscyamus pusillus* L., Egypt, *Abdel-Migid s.n.* (WTU), EU580891/EU580998; *Ioichroma australe* Griseb., Bolivia, *Olmstead S-17* (WTU), EU580892/EU580999; *Ioichroma cardenasianum* Hunz., Bolivia, *Smith & al.* 383 (WIS), EU580893/EU581000; *Ioichroma fuchsoides* (Bonpl.) Miers, Colombia, *Olmstead S-29* (WTU), EU580894/EU581001; *Ioichroma umbellatum* (Ruiz & Pav.) D'Arcy, Peru, *Hutchison & al.* 6240 (UC), EU580895/EU581002; *Jaborosa integrifolia* Lam., Argentina, BIRM S.0290/83 (BIRM), EU580896/EU581003; *Jaborosa sativa* (Miers) Hunz. & Barboza, Argentina, BIRM S.0234 (BIRM), EU580897/EU581005; *Jaborosa squarrosa* (Miers) Hunz. & Barboza, Bolivia, *Nee & al.* 51819 (NY), EU126013/EU581004; *Jaltomata auriculata* (Miers) Mione, Andean South America, BIRM S.1596/76 (BIRM), EU580898/EU581006; *Jaltomata grandiflora* (B.L. Rob. & Greenm.) D'Arcy, Mione, & T. Davis, Mexico, *D'Arcy* 17709 (probably *D'Arcy* 17749, grown at MO from seed of *Tilton Davis* 1114), EU580899/EU581007; *Jaltomata procumbens* (Cav.) J.L. Gentry, Mexico, *Olmstead S-24* (WTU), U47429/AY098695; *Jaltomata sinuosa* (Miers) Mione, Bolivia, *Nee & al.* 51830 (NY), EU580900/DQ180418; *Juanulloa mexicana* (Schltldl.) Miers, Mexico, BIRM S.0411/69 (BIRM), U08919/EU581008; *Larnax subtriflora* (Ruiz & Pav.) Miers, Peru, *Sawyer* 777 (CONN), EU580902/EU581009; *Larnax sylvarum* (Standl. & C.V. Morton) N.W. Sawyer, Costa Rica, *Bohs* 2504 (UT), EU126022/-; *Larnax sylvarum* (Standl. & Morton) N.W. Sawyer, Costa Rica, *Almeda* 2226 (DUKE), -/EU580985; *Latua pubiflora* (Griseb.) Baill., Chile, *Gardner & al.* DCI 20 (E), EU580903/EU581010; *Latua pubiflora* (Griseb.) Baill., Chile, *Plowman* 2643 (WIS), -/EU581011; *Leptoglossis darciana* Hunz. & Subils, Peru, *Dillon & Dillon* 3684 (US), EU580904/EU581012; *Leucophysalis grandiflora* (Hook.) Rydb., U.S.A., *Olmstead S-30* (WTU), EU580905/EU581013; *Leucophysalis nana* (A. Gray) Averett, U.S.A., *Bartholomew* 5994 (MO), EU580906/EU581014; *Lycianthes biflora* (Lour.) Bitter, China, *Guosheng* 6316 (MO), DQ667551/EU581015; *Lycianthes ciliolata* (M. Martens & Galeotti) Bitter, Mexico, *Dean* 206 (DAV), DQ667553/EU581016; *Lycianthes glandulosa* (Ruiz & Pav.) Bitter, Andean South America, BIRM S.1616/75 (BIRM), DQ667560/EU581017; *Lycianthes heteroclitia* (Sendtn.) Bitter, Costa Rica, *Bohs* 2376 (UT), U72756/DQ180414; *Lycianthes inaequilatera* (Rusby) Bitter, Bolivia, *Bohs* 3089 (UT), DQ667561/EU581018; *Lycianthes multiflora* Bitter, Costa Rica, *Bohs* 2902 (UT), DQ667567/EU581019; *Lycianthes peduncularis* (Schltldl.) Bitter, Mexico, *Dean* 283 (DAV), DQ667570/EU581020; *Lycianthes rantonnei* (Carrière) Bitter, Argentina, Brazil, Paraguay, *Olmstead S-96* (WTU), BIRM S.0928 (BIRM), AF500840/DQ180417; *Lycianthes shanesii* (F. Muell.) A.R. Bean, SE Asia; cult. by W; D'Arcy (MO), *Bohs* 2721 (UT), DQ667578/EU581021; *Lycium barbarum* L., China, *Olmstead S-35* (WTU), EU580907/AB036601 & AB036572; *Lycium cestroides* Schltldl., Argentina, BIRM S.0368/70 (BIRM), *Olmstead S-34* (WTU), U08920/AB036578 & AB036607; *Lycium pallidum* Miers, U.S.A., *Olmstead* 95-14 (WTU), EU580908/AB036584 & AB036613; *Lycium sandwicense* A. Gray, Hawaii, *Olmstead* 92-224 (WTU), EU580909/EU581022; *Mandragora caulescens* C.B. Clarke, Asia, *Ho & al.* 1172 (GH), EU580911/EU581023; *Mandragora officinarum* L., Mediterranean, BIRM S.0672 (BIRM), U08922/EU581024; *Margaranthus solanaceus* Schltldl., Mexico, *Olmstead S-37* (WTU), EU580912/EU581025; *Markea panamensis* Standl. 1, Panama, BIRM S.1462/73 (BIRM), EU580883/EU581026; *Markea panamensis* Standl. 2, Panama, *Knapp & Mallet* 9164 (BM), EU580885/EU581027; *Markea ulei* (Dammer) Cuatrec., Brazil, *Bohs* 3061 (UT), EU126021/EU581028; *Melananthes guatemalensis* (Benth.) Soler., Guatemala, *King* 1930 (US), EU580913/EU581029; *Melissia begoniifolia* Hook. f., St. Helena, *Cronk s.n.* (E), EU580914/-; *Merinthopodium neuranthum* (Hemsl.) Donn. Sm., Costa Rica, *Bohs* 2490 (UT), EU126014/EU581030; *Metternichia principis* J.C. Mikan, Brazil, *Schnoor* 88 (MO), AY206748/AY206763 & AY206729; *Nectouxia formosa* Kunth, Mexico, *Bye* 4308 (MO), EU580915/EU581031; *Nicandra physalodes* (L.) Gaertn., Peru, *Olmstead S-38* (WTU); U08924/EU581032; *Nicotiana acuminata* (Graham) Hook., Argentina/Chile, *Olmstead S-39* (WTU) BIRM S.0372 (BIRM), U08923/AY098696; *Nicotiana africana* Merxm., Namibia, *Clarkson* 020 (BM), AJ585943/AJ577448; *Nicotiana glauca* Graham, Argentina, *Nee & al.* 51725 (BM), AJ585910/AJ577414; *Nicotiana glutinosa* L., Peru, BIRM S.1002 (BIRM), AY098726/AY098699; *Nicotiana gossei* Domin, Australia, *Olmstead S-48* (WTU), BIRM S.1003 (BIRM), AY098727/AY098700; *Nicotiana paniculata* L., Peru, *Olmstead S-53* (WTU), BIRM S.0560 (BIRM), AY098728/AY098701; *Nicotiana suaveolens* Lehm. var. *excelsior* J.M. Black, Australia, *Olmstead S-44* (WTU), BIRM S.0904 (BIRM), AY098725/AY098698; *Nicotiana tabacum* L., in cult., no voucher, L14953/Z00044; *Nierembergia andina* Millán, Argentina, *Nee & Bohs* 50842 (NY), EU126015/-; *Nierembergia hippomanica* Miers, Argentina, *Olmstead S-58* (WTU), EU580917/EU581033; *Nolana linearifolia* Phil., Chile, *Dillon & Dillon* 5727 (F),

Appendix. Continued.

EU580918/EU581034; *Nolana paradoxa* Lindl., Chile, Freyre s.n. (F), EU580919/EU581035; *Nolana spathulata* Ruiz & Pav., Peru, Dillon & Dillon 3767 (F), U08925/EU581036; *Nothoecstrum latifolium* A. Gray, Hawaii, Herbst & al. 725 (COLO), EU580921/EU581037; *Nothoecstrum longifolium* A. Gray, Hawaii, Oppenheimer s.n.; (BISH), EU580922/EU581038; *Oryctes nevadensis* S. Watson, U.S.A., Tiehm 11982 (COLO), EU580923/EU581039; *Pantacantha ameghinoi* Speg., Argentina, Ambrosetti & al. 1419 (CORD), EU580924/EU581040; *Petunia axillaris* (Lam.) Britton, Sterns, & Poggenb., Southern Brazil to Northern Argentina, Olmstead S-60 (WTU), BIRM S.0367/68 (BIRM), U08926/AY098702; *Phrodus microphyllus* (Miers) Miers, Chile, Simon 484, 10/29/70, (UC), EU580925/EU581041; *Physalis alkekengi* L., Asia, D'Arcy 17707 (MO), U08927/DQ180420; *Physalis carpenteri* Rydb., U.S.A., Whitson 1133 (DUKE), EU580926/EU581042; *Physalis heterophylla* Nees, U.S.A., Olmstead S-64 (WTU), EU580927/EU581043; *Physalis peruviana* L., Peru, Olmstead S-69 (WTU), EU580928/EU581044; *Physalis philadelphica* Lam., in cult., Bohs 2433 (UT), EU580929/EU581045; *Physochlaina infundibularis* Kuang, China, Boufford & al., 26096 (A), EU580930/EU581046; *Physochlaina orientalis* (Bieb.) G. Don, Russia, BIRM S.0125/71 (BIRM), EU580931/EU581047; *Plowmania nyctaginoides* (Standl.) Hunz. & Subils, Mexico, Breedlove & Bartholomew 55920 (MO), EU580932/EU581048; *Protoschwenkia mandonii* Soler., Bolivia, Nee & Solomon 32037 (US), EU580934/–; *Protoschwenkia mandonii* Soler., Bolivia, Nee & al. 51827 (NY), EU126023/EU581049; *Przewalskia tangutica* Maxim., China, Ho & al. 505 (GH), EU580935/EU581050; *Quincula lobata* (Torr.) Raf., U.S.A., Olmstead 93-74 (WTU), EU580936/EU581051; *Salpichroa oranifolia* (Lam.) Baill., South America, Olmstead S-70 (WTU), BIRM S.0291 (BIRM), EU580937/EU581052; *Salpiglossis sinuata* Ruiz & Pav., Chile, Olmstead S-71 (WTU), BIRM S.0181/69 (BIRM), U08928/AY206765 & AY206730; *Saracha punctata* Ruiz & Pav., South America, Plowman 4651 (UC), EU580938/EU581053; *Schizanthus grahamii* Gill. ex Hook., Argentina, Olmstead 2004-199 (WTU), EU580939/EU581054; *Schizanthus pinnatus* Ruiz & Pav., Chile, Olmstead S-72 (WTU), BIRM S.0224/66 (BIRM), U08929/AY206766; *Schultesianthus leucanthus* (Donn. Sm.) Hunz., Mexico, Wendt 6784 (TEX), EU580940/EU581055; *Schultesianthus megalandrus* (Dunal) Hunz., Ecuador, Acevedo & al. 1715 (US), EU580941/EU581056; *Schwenkia glabrata* Kunth, Venezuela, Benitez de Rojas 3992 (MO), EU580942/EU581057; *Schwenkia lateriflora* (Vahl) Carvalho, Venezuela, Benitez de Rojas 3901 (MO), AY206749/AY206767; *Sclerophylax adnatifolia* Di Fulvio, Argentina, Nee & Bohs 50857 (NY), EU126016/EU581058; *Sclerophylax gilliesii* Miers, Argentina, Bartlett s.n. (UC), EU580943/EU581059; *Scopolia carniolica* Jacq., Europe, specimen uncertain (GH), EU580944/–; *Scopolia carniolica* Jacq., Europe, specimen uncertain (MO), –/EU581060; *Scopolia japonica* Maxim., Japan, Tsugaru & Sawada 17731 (A), EU580945/–; *Scopolia japonica* Maxim., Japan, Akiyama s.n. (MO), –/EU581061; *Sessea corymbiflora* Goudet ex R. Taylor & R. Phillips, Venezuela, Benitez de Rojas 5373 (MY), AY206750/AY206768; *Solanandra brachycalyx* Kuntze, Costa Rica, Plowman & Gentry 2957 (MO), EU580946/EU581062; *Solanandra grandiflora* Sw., Caribbean and South America, in cult., Matthei Bot. Gard., #840415 (no voucher), U08930/EU581063; *Solanum abutiloides* (Griseb.) Bitter & Lillo, Argentina, Bolivia, Olmstead S-73 (WTU), BIRM S.0655 (BIRM), U47415/AY555453; *Solanum aviculare* G. Forst., Australia, BIRM S.0809 (BIRM), U47418/AY559238; *Solanum betaceum* Cav., Bolivia, Bohs 2468 (UT), U47428/DQ180426; *Solanum dulcamara* L., U.S.A., no voucher, U47419/AY266231; *Solanum herculeum* Bohs, Morocco, Jury 13742 (RNG), AF224065/DQ180466; *Solanum lycopersicum* L., in cult., no voucher, U08921/AY098703; *Solanum melongena* L., Africa, Olmstead S-91 (WTU), BIRM S.0657 (BIRM), AF224069/DQ180406; *Solanum pseudocapsicum* L., Central and South America, BIRM S.0870 (BIRM), U47422/DQ180436; *Solanum torvum* Sw., Mexico, Central America, Olmstead S-101 (WTU), BIRM S.0839 (BIRM), L76286/AY266246; *Solanum trisetum* Dunal, France, Bohs 2718 (UT), AF22406/DQ180471; *Solanum wendlandii* Hook. f., Central America, BIRM S.0488/67 (BIRM), U47427/DQ180440; *Streptosolen jamesonii* (Benth.) Miers, Ecuador/Peru, Olmstead S-106 (WTU), EU580948/EU581064; *Symonanthus aromaticus* (C.A. Gardner) Haegi, Australia, McKinney s.n. herb. uncertain (UWA), (PERTH), or (KPBG), AY098723/AY098693; *Symonanthus bancroftii* (F. Muell.) Haegi, Australia, Stace s.n. (KPBG), AY098724/AY098694; *Tsoala tubiflora* Bosser & D'Arcy, Madagascar, Res. Nat. 2918, Ramamonjisoa (P), EU580949/EU581065; *Tubocapsicum anomalum* (Franch. & Sav.) Makino, China, Chen 231 (MO), EU580950/EU581066; *Vassobia dichotoma* (Rusby) Bitter, Bolivia, Nee & al. 51797 (NY), EU126017/EU581067; *Vestia foetida* (Ruiz & Pav.) Hoffmanns., Chile, BIRM S.0105 (BIRM), AY206751/AY206769; *Withania coagulans* (Stocks) Dunal, Central Asia, Olmstead S-109 (WTU), EU580951/EU581068; *Withania somnifera* (L.) Dunal, Canary Is., Mediterranean to Central Asia, Voucher unknown; in cult. at U. Connecticut Greenhouse (#199200148), EU580952/EU581069; *Witheringia cuneata* (Standl.) Hunz., Costa Rica, Bohs 2394 (UT), EU126018/EU581070; *Witheringia macrantha* (Standl.) & C.V. Morton) Hunz., Costa Rica, Bohs 2512 (UT), EU126019/EU581071; *Witheringia meiantha* (Donn. Sm.) Hunz., Costa Rica, Bohs 3015 (UT), EU126020/EU581072; *Witheringia mexicana* (B.L. Rob.) Hunz., Mexico, BIRM S.1199 (BIRM), EU580953/EU581073; *Witheringia solanacea* L'Hér., Costa Rica, Bohs 2416 (UT), U72755/EU581074.

Outgroups: *Montinia caryophyllacea* Thunb., South Africa, Olmstead 94-01 (WTU), AF130178/AY206764; *Ipomoea batatas* (L.) Lam., unknown, K.-J. Kim 13844 (YNUH), AF130177/–; *Ipomoea batatas* (L.) Lam., Costa Rica, Stefanovic 00-20 (WTU), –/AY101071; *Convolvulus arvensis* L., U.S.A., Olmstead 92-244 (WTU), AJ236243/AY101102; *Evolvulus glomeratus* Nees & C. Mart., Brazil, Olmstead 92-215 (WTU), AY936341/AY101121; *Dinetus truncatus* (Kurz) Staples, Thailand, Staples & al. 425 (A), AY93634/AY101162.