Phylogeny and Provisional Classification of the Solanaceae Based on Chloroplast DNA

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Abstract

A phylogenetic analysis of the Solanaceae based on chloroplast DNA variation is presented. Restriction site maps were determined for 79 species (52 genera) for 11 restriction enzymes. Sequences of two chloroplast genes, rbcL and ndhF, were determined for 30 and 36 species respectively, including six genera not sampled in the restriction site survey. The results are presented as three separate analyses examining relationships at different hierarchical levels. The resulting cladograms provide the basis for a provisional new infrafamilial classification. This classification includes seven subfamilies, three of which are further subdivided into tribes, two of which are further subdivided into subtribes. This classification is compared to the contemporary classification of Hunziker et al. (this volume).

Introduction

The roots of modern plant classification spread deeply into the history of western civilization, but the starting point for modern classification and nomenclature dates to Linnaeus (1753). Linnaeus held a typological view of species, consistent with the belief in special creation prevalent at the time, but he grouped species by similarities into a hierarchical classification. However, Darwin (1859) first understood that a hierarchical classification has a biological foundation in the evolutionary history that connects species in the form of a phylogenetic tree. For more than a century, taxonomists have pursued Darwin's goal of "all true classification being genealogical." Many of the groups recognized in Linnaeus' work (1753) are included in classifications today, because the similarities he recognized represent homologies and reveal evolutionary history.

Progress toward the goal of producing phylogenetic classifications has accelerated greatly in recent years due to three advances: 1) an explicit framework for interpreting phylogeny (Hennig 1966); 2) the incorporation of modern methods from molecular biology that take advantage of the enormous amount of data available in the DNA of organisms; and 3) the development of computer technology that has allowed the analysis of such large amounts of data. Revised classifications reflecting these principles and methods have appeared for the Lamiaceae (Cantino et al. 1992) and Asteraceae (Bremer & Jansen 1992).

The history of Solanaceae classification (D'Arcy 1979, 1991) is typical of many large families of flowering plants (e.g., Scrophulariaceae, reviewed in Olmstead & Reeves 1995) in having a core of genera assigned to the family in essentially all treatments and a number of allied genera or groups of genera that are alternatively treated as either belonging to the family, belonging to other related families, or segregated into their own families. Often these latter taxa exhibit unusual combinations of characters found in another family or lack characters typical of the family. It is these problematic taxa for which molecular data often prove most helpful (Keeley & Jansen 1991; Olmstead & al. 1993a; Bremer & al. 1994; Olmstead & Reeves 1995). Examples of problematic genera in the history of classification of the Solanaceae include the zygomorphic-flowered members of the polyphyletic tribe Salpiglossidae, placed in the Scrophulariaceae by Bentham (1876), Nolana, placed in its own family in many treatments (e.g., Thorne 1992), and Goetzea and related genera, also placed in their own family in most treatments (e.g., D'Arcy 1991; Thorne 1992). In addition there are several enigmatic and rarely collected genera, including Atrichodendron, Duckeodendron, Lithophytum, Parabouchetia, Paiuia, Sclerophylax,

and Tsoala, whose affinities to the Solanaceae are debated (D'Arcy 1991; Hunziker & al., this volume).

Chloroplast DNA (cpDNA) has proven to be an excellent source of molecular variation available for higher order (i.e., generic level and above) phylogenetic studies in plants (Olmstead & Palmer 1994). Features of cpDNA especially useful in phylogeny reconstruction include its conservative rate of sequence and structural evolution (Wolfe & al. 1987; Palmer 1991), its large yet managable size, relative to animal mitochondrial DNA, and compared to nuclear DNA, the lack of independently evolving duplicated genes (Olmstead & Palmer 1994). The chloroplast genome of Nicotiana tabacum was the first to be completely sequenced of any flowering plant (Shinozaki & al. 1986) and has a total length, with subsequent corrections (Olmstead & al. 1993b), of 155,952 base pairs. Having a reference genome within the family that is completely sequenced makes comparative study of cpDNA in the Solanaceae very reliable. Many of the systematic advances made through the study of cpDNA are summarized in recent reviews (Palmer & al. 1988; Soltis & al. 1992; Clegg 1993; Doyle 1993; Sytsma & Hahn 1994; Soltis & Soltis, 1995).

Data from the study of cpDNA have helped to resolve some long-standing problems in Solanaceae systematics. The Convolvulaceae are now established as the sister group to the Solanaceae; together these families comprise the order Solanales (Olmstead & al. 1992; 1993). Studies of cpDNA have clarified phylogenetic relationships in Solanum (Palmer & Zamir 1982; Hosaka & al. 1984; Spooner & al. 1993; Bohs & Olmstead, this volume; Olmstead & Palmer, this volume; and Bruneau & Dickson, personal communication), Nicotiana (Kung & al. 1982; Olmstead & Palmer 1991), Jaltomata (Mione & al. 1994), and Physalis and related genera (Mione & al. 1994; Martinez & al., in press). Two previous studies have examined relationships of the entire family (Olmstead & Palmer 1992; Olmstead & Sweere 1994). In these studies, subfamily Solanoideae was shown to be monophyletic (if Nolana is included), whereas the Cestroideae (sensu D'Arcy 1991) are a paraphyletic ancestral grade within the family. Tribes Nicotianeae, Salpiglossideae, and Solaneae (sensu D'Arcy 1991) are polyphyletic. A novel monophyletic group consisting of the Anthocercideae, Nicotiana, and the Solanoideae was identified and characterized as the "X=12" clade in recognition of the base chromosome number, a synapomorphy for the group. This previously unidentified group is the most strongly supported major infrafamilial group based on cpDNA evidence (Olmstead & Palmer 1992; Olmstead & Sweere 1994).

Phylogenetic analyses relying on traditional systematic characters have been carried out on several suprageneric groups in the Solanaceae, including tribes Datureae (Knapp & Persson, this volume), Juanulloeae (Persson & al.1994), and Schwenckieae (D'Arcy & Benitez de Rojas 1991). However, no comprehensive morphological phylogenetic analysis encompassing the entire family is available for comparison with the cpDNA study of Olmstead & Palmer (1992) or that presented here.

The goal of this paper is to summarize our phylogenetic findings based on a large body of new cpDNA data and to present a provisional classification based on those findings following principles of phylogenetic classification (deQueiroz & Gauthier 1992) and the example set by Cantino & al. (1992). A comparison is made with the contemporary classification of Hunziker & al. (this volume).

Methods

Two different methods of assessing cpDNA variation were used in this study: 1) restriction site analysis of the entire chloroplast genome and 2) DNA sequencing of two genes, rbcL (encoding the large subunit of the photosynthesis enzyme rubisco) and ndhF (encoding a subunit of the chloroplast NADH dehydrogenase). Data acquisition and analysis for each method are detailed elsewhere (restriction sites - Olmstead & Palmer 1992; sequencing - Olmstead & al. 1992, 1993a; Olmstead & Sweere 1994). The genes rbcL and ndhF have been compared most extensively for systematic purposes in the Solanaceae and related families (Olmstead & al. 1993a; Olmstead & Sweere 1994; Olmstead & Reeves 1995; Scotland & al. 1995) and together provide approximately 3500 base pairs (bp) of sequence for comparison (total lengths are 1434 and 2223 bp in rbcL and ndhF, respectively, in Nicotiana tabacum).

The data compiled for these analyses represent one of the largest cpDNA data sets for any family of flowering plants. A total of 136 accessions was included in the cpDNA survey on which this study is based, although only 92 are included in the analyses presented here (Table 1). The remaining accessions represent multiple species of Nicotiana and Solanum, which are included in separate studies (Olmstead & Palmer 1991, this volume). Restriction site data are available for 124 species of Solanaceae, including two accessions of Datura stramonium, and for two outgroup species in the sister family Convolvulaceae, Ipomoea coccinea and Calonyction aculeatum (= Ipomoea bona-nox). The DNA of the latter species did not cut well for some enzymes and the regions successfully mapped for both outgroup species are very similar in their cpDNA restriction site maps, so for purposes of the phylogenetic analysis, they are scored as a single taxon (the few informative restriction sites that differ between them are scored as unknown for the outgroup and sites that are unique to either of them are scored as autapomorphies of the outgroup). DNA sequence data for both rbcL and ndhF are available for 30 species, including eight for which restriction site data are not available, and ndhF sequences were determined for six additional species, including one, Browallia eludens, for which this is the only source of data. Two outgroup species, Ipomoea coccinea and Montinia caryophyllacea have been sequenced for both genes.

The restriction site analysis surveyed the presence or absence of recognition sequences for ten restriction enzymes (Bam HI, Ban II, Bcl I, Bgl II, Cla I, Eco O109I, Eco RI, Eco RV, Hind III, and Xba I) in all 126 species and an additional enzyme (Dra I) for 32 species. A total of 1358 restriction sites was compared, representing over 8000 bp of cpDNA, or approximately 6.2% of the total chloroplast genome if only one copy of the inverted repeat is considered. The analyses described below include various subsets of the complete taxonomic sample with limited sampling in the two large genera Nicotiana and Solanum (see Olmstead & Palmer 1991; this volume). The rbcL comparisons include 1408 bp of aligned sequence (no gaps were found) and the ndhF sequences include 2134 bp of aligned sequence (2086 bp in tobacco plus 48 bp of gaps inserted in the sequence alignment to account for length variation in some sequences relative to tobacco). Missing characters exist in the data set for several reasons. In the restriction site data, restriction sites that are mapped to a region of the chloroplast genome that is deleted in one or more taxa relative to others are scored as missing in the taxon with the deletion. Similarly, in the DNA sequences, deleted regions (found only in ndhF) are scored as missing for those taxa with the deletions. Also in the restriction site data, sites that are unable

to be mapped unambiguously to the same location as sites mapped in other taxa, due to insertions or deletions, or insertions or deletions in combination with numerous restriction site mutations in the vicinity, are scored as missing. The outgroup, Ipomoea, is affected most by this latter source of missing data.

Due to the partially overlapping nature of the data set (e.g., some pairs of taxa have no characters in common), the phylogenetic inference is presented in the form of three separate analyses designed to make use of all of the data and to emphasize different hierarchical levels in the family. In each analysis, all included taxa are sampled for one source of data (sequences or restriction sites) and the alternate source of data is included for those taxa in which it is available. The first two analyses examine relationships at the broadest level within the family and the third examines relationships within the large and monophyletic "X=12" clade (Olmstead & Palmer 1992).

All phylogenetic analyses were done using the heuristic search option (TBR branch swapping; MULPARS "on") in PAUP vers. 3.1.1 (Swofford 1993) with 100 replicate searches, in which a different, randomly-generated tree was used to start each search. All changes were weighted equally. Bootstrap analyses were conducted to examine relative levels of support for clades within trees. Bootstrapping was performed using 200 replicates (33 replicates for the third analysis) with the heuristic search option.

In the results and their discussion that follow, inferences regarding relationships within the Solanaceae will be related to a provisional synoptical classification (Appendix I, Figs. 2, 4, 6), which is based on principles of phylogenetic classification (deQueiroz & Gauthier 1992). Primary among the principles on which a phylogenetic classification must be based is the recognition that named groups, or taxa, represent evolutionary lineages, not groups of organisms defined by the possession of certain characteristics. Named suprageneric taxa in the following discussion refer to the accompanying provisional classification, unless otherwise noted.

Results and Discussion

Phylogenetic Analyses

The first analysis includes 32 species of Solanaceae and two outgroups, all of which have DNA sequence data available. Restriction site data are included where available (26 species). A total of 750 characters provide phylogenetic information for this analysis (i.e., at least two states present in at least two taxa each). The analysis of this data set identified 12 equally most-parsimonious trees of 3060 steps (consistency index, CI, including/excluding autapomorphies = 0.66/0.48). Branch lengths are indicated on the majority-rule consensus tree (Fig. 1), which also is one of the 12 equal length trees. Division of the family into provisional subfamilies is indicated on the strict consensus tree (Fig. 2). Gaps in the ndhF sequences within the Solanaceae and their direction of evolution (deletion or insertion) are indicated on Figure 2. Three insertions within the Solanaceae are unique to individual taxa, whereas two nine bp deletions are inferred to have occurred in the common ancestor of the clade represented by Bouchetia, Hunzikeria, and Nierembergia. Because insertions and deletions in chloroplast gene sequences are rare events relative to nucleotide substitutions, they often provide strong indication of relationship (Johnson and Soltis 1995; Scotland et al. 1995). The fact that the group comprising these

three taxa is identified by nucleotide substitutions and is supported by two deletions makes a strong case for the monophyly of this group within the Petunioideae. In these results, the Solanoideae and Nicotianoideae (here including Nicotiana and the Anthocercideae) each are monophyletic and together form the monophyletic "X=12" group. Progressively deeper branches include the Petunioideae, Cestroideae, Goetzeoideae, Schizanthoideae, and Schwenckioideae. However, confidence in the branching order among the groups outside the "X=12" clade is low as indicated by the bootstrap values associated with them on Figure 2. The basal branches represent small, homogeneous groups (e.g., 6-30 species) for which a single species should provide sufficient sampling. The fact that the branch order among these lineages is uncertain (e.g., low bootstrap values) suggests the conservative conclusion of recognizing distinct monophyletic subfamilies, rather than uniting any of them into a group that may not be monophyletic.

The second analysis includes 34 species of Solanaceae and the outgroup Ipomoea; restriction site data are available for all taxa in this data set and sequence data are available for 25 species. The second analysis includes the same representatives within the large "X=12" clade that are included in the first analysis, except for Oryctes, which is included in the first analysis and not in the second, and includes all of the species outside of the "X=12" clade for which restriction site data are available. A total of 655 characters provide phylogenetic information for this analysis. The analysis of this data set identified eight equally most-parsimonious trees of 2698 steps (CI = 0.65/0.43). Branch lengths are indicated on the majority-rule consensus tree (Fig. 3). Division of those taxa not in the "X=12" clade into provisional subfamilies and tribes is indicated on the strict consensus tree (Fig. 4). Taxon sampling is somewhat different between the first two analyses, resulting in an emphasis on sequence over restriction site data in the former (447 sequence vs. 303 restriction site characters) and the converse in the latter analysis (213 vs. 442). However, the results of the two analyses are completely consistent with respect to relationships among groups. Goetzea and Schwenckia were not included in the restriction site analysis, so are not available for comparison with Schizanthus at the base of this tree.

The third analysis includes 66 species belonging to the "X=12" clade and two outgroup species (Petunia axillaris and Brunfelsia americana). Restriction site data are included for all species and sequence data for 24 of them. A total of 595 characters provides phylogenetic information for this analysis. The smaller number of informative characters in this analysis, despite the larger number of taxa, reflects the closer relationships among the included taxa. The analysis of this data set identified 108 equally most-parsimonious trees of 2245 steps (CI = 0.58/0.40). Branch lengths are indicated on the majority-rule consensus tree (Fig. 5) and division of the "X=12" clade into provisional subfamilies, tribes, and subtribes is indicated on the strict consensus tree (Fig. 6).

The Nicotianoideae and Solanoideae represent the basal split within the "X=12" clade. Within the former, tribe Nicotianeae (represented here and possibly consisting solely of Nicotiana) is sister to the Australian endemic tribe Anthocercideae. Within the Solanoideae, the basal branch consists of tribes Hyoscyameae, Lycieae, Nolaneae, and Jaborosae, with the Hyoscyameae sister group to a clade composed of the other three. The second basal-most branch in the Solanoideae weakly unites the very divergent Mandragora (Mandragoreae) with the Solandreae, which is provisionally divided into two subtribes, Juanulloinae and

Solandrinae. The next branch weakly unites Nicandra and Exodeconus. Nicandra traditionally is placed in its own tribe (D'Arcy 1991) and Exodeconus in the Solaneae. The Datureae form the next branch and are the sister group to a large clade comprising most of the traditional Solaneae (Hunziker 1979; D'Arcy 1991; Hunziker & al., this volume). The traditional Solaneae (Solaneae s.l.) comprises an enormous portion of the family and probably is not monophyletic as traditionally circumscribed (e.g., D'Arcy 1991). The cpDNA results provide the first evidence for dividing this group along phylogenetic lines. The suggested classification here includes a much reduced Solaneae, including Solanum s.l. (with Lycopersicon and Cyphomandra) and Jaltomata, a new tribe Capsiceae, represented here by Capsicum and New World species of Lycianthes, and a new large tribe Physaleae, which is further divided into four subtribes: Iochrominae, Physalinae, Salpichroinae, and Withaninae. The results of this analysis are incongruent with the results of the first two analyses with respect to the position of some taxa within the Solanoideae. In the first two analyses, Physalis and Oryctes are the sole representatives of the large tribe Physaleae and are inferred to be most closely related to Datura (Datureae), whereas in the third analysis, with much greater sampling within the Solanoideae, the Physaleae are sister group to the Capsiceae. In the third analysis, Jaltomata is sister to Solanum, whereas in the previous analyses Capsicum is sister to Solanum.

Implications For Classification

The accompanying provisional synoptical classification of the Solanaceae is an attempt to apply phylogenetic principles to the taxonomy of the family at the suprageneric level. No judgement has been made with respect to the status of individual genera (names of accepted genera generally follow D'Arcy 1991). In the discussion below, mention will be made of cases where current generic circumscriptions may need to be revised to reflect phylogenetic lines. Much detailed work remains to produce a phylogenetic classification at the generic level. Additional phylogenetic study and nomenclatural research is required before a revised classification can be published, therefore this attempt remains provisional.

The application of phylogenetic principles to taxonomy of the Solanaceae will result in a classification that is more predictive with respect to interpreting evolution in the family. An example identified previously (Olmstead & Palmer 1992) illustrates this point. If Nolana is recognized as its own family (e.g., Thorne 1992) or subfamily (e.g., D'Arcy 1991), the observation of similarities in wood anatomy (Carlquist 1987) and calyx vasculature (Armstrong 1986) between it and Lycium (Solanoideae) appear as anomalous results, most likely interpreted as convergence. However, if Nolana is recognized at the tribal level, equivalent with tribe Lycieae, within subfamily Solanoideae, the observations are much more readily recognized as potential homologies of the two taxa.

Recognizing evolutionary lineages (in the practical sense, monophyletic groups of extant organisms) as taxa in a classification changes the emphasis from associating a taxon name with a characteristic or set of characteristics to associating a name with a lineage (deQueiroz & Gauthier 1992). This change promotes nomenclatural stability by shifting the critical basis for taxon names away from one author's perception of important characteristics, which may be different from another author's perception, to their association with a clade. As our ability to circumscribe monophyletic groups improves, or as additional information (in the form of characters or taxa), is added, the composition of a group may change, but the name

and its underlying evolutionary significance remain stable. Subfamily Cestroideae provides an example. The traditional subfamily Cestroideae (D'Arcy 1991) represents a paraphyletic group due to the exclusion of subfamily Solanoideae (Olmstead & Palmer 1992). The largest monophyletic group to which the name Cestroideae can be applied (while keeping the convention of retaining the type genus in the group) is indicated in Figures 2 and 4. Further refinement of our understanding of relationships may indicate that one or more of the genera related to Cestrum does not belong to the same exclusive monophyletic group, but the name Cestroideae will remain tied to the monophyletic group to which the genus belongs, thereby providing both stability in the face of future observations and consistency with respect to implications of evolutionary history in the group. Decisions regarding rank within the hierarchy at which to apply names will remain subjective, as they have in traditional classifications, and for practical purposes are best made in accord with established usage.

The most evident change resulting from an adherence to phylogenetic principles in the accompanying classification, relative to traditional classifications of the Solanaceae, is the splitting of the traditional Cestroideae (e.g., sensu D'Arcy 1991) into five smaller, monophyletic subfamilies. Most of the rest of the changes in classification made here represent new insights regarding relationships within the family. This includes the confirmation that the small group of Antillean genera, Coeloneurum, Espadaea, Goetzea, and Henoonia (represented by Goetzea in this study), which often is excluded from the Solanaceae (D'Arcy 1991; Thorne 1992), belongs within the family and is recognized here as subfamily Goetzeoideae. In the Goetzeoideae, and elsewhere in the accompanying classification, redundant classes are omitted (e.g., no tribe Goetzeae is established); exceptions are restricted to monogeneric groups. Similarly, Nolana, often recognized as a distinct family (e.g., Thorne 1992), is shown to be embedded well within the Solanaceae (Olmstead & Palmer 1992) and is recognized here as a tribe in subfamily Solanoideae.

Elements of the traditional Cestroideae now recognized as subfamilies include: Schwenckioideae (former tribe Schwenckieae), Schizanthoideae (Schizanthus, formerly in tribe Salpiglossideae), Cestroideae (former Cestreae and part of Salpiglossideae), Petunioideae (most of former Nicotianeae and Brunfelsia of the Salpiglossideae), and Nicotianoideae (Nicotiana and tribe Anthocercideae). The first two of these subfamilies (Schwenckioideae and Schizanthoideae), along with the Goetzeoideae, are small homogeneous groups represented by a single taxon in this analysis. The Cestroideae provisionally includes three tribes, the Cestreae, which is similar to traditional circumscriptions of the tribe, Browallieae, and Salpiglossideae. The latter two tribes include genera that were included in the polyphyletic traditional Salpiglossideae (Olmstead & Palmer 1992). The Petunioideae includes all of the former Nicotianeae plus Brunfelsia, but excludes Nicotiana. A clade represented in the cpDNA results by Bouchetia, Hunzikeria, and Nierembergia is very distinct from Petunia on the basis of sequence data (Figs. 1-2), but none of the taxa were included in the restriction site survey. Conversely, Brunfelsia is distinct from Petunia on the basis of restriction site data (Figs. 3-4), but has not been included in the sequencing study. Additional work in progress should determine whether designating tribal groups within the Petunioideae is appropriate.

Subfamily Nicotianoideae includes two tribes, Nicotianeae (Nicotiana only) and Anthocercideae, which is endemic to Australia. This group was first identified on the basis of cpDNA (Olmstead & Palmer 1992), but evidence supporting the segregation

of Nicotiana from Petunia and from the rest of the traditional tribe Nicotianeae is available from sequence comparisons of nuclear ribosomal ITS regions (Price, this volume) and limited taxonomic sampling of sequences for the nuclear gene rbcS (Meagher & al. 1989). In fact, cpDNA provides strong evidence indicating the close relationship of this subfamily to the Solanoideae, and this conclusion is supported further by the common base chromosome number for both subfamilies of X=12. The fact that the two tribes in this subfamily share a distribution in Australia does not indicate a common origin there, however. Nicotiana is represented in Australia by a derived group of species, apparently the result of a recent colonization (Olmstead & Palmer 1991), whereas the entire, molecularly diverse Anthocercideae is restricted to Australia, suggesting an ancient colonization of Australia (Olmstead & Palmer 1992).

Subfamily Solanoideae is divided into 11 tribes (including Nolaneae), one of which contains four subtribes. Each of the tribes and subtribes is well-supported by the cpDNA data and relationships among all named groups are resolved in Figures 5-6. However, in only a few cases are relationships among tribes evident and most of the relationships among major groups in the Solanoideae are not clearly delineated.

A group comprising the Hyoscyameae, Jaboroseae, Lycieae, and Nolaneae forms the sister group to the rest of the Solanoideae (Figs. 5-6) in the most parsimonious trees. This sister group relationship is not strongly supported (four steps/42% bootstrap), but the grouping of these four tribes is well supported (13 steps/97% bootstrap). The molecular evidence clearly supports a placement of Atropa with the Hyoscyameae (97% bootstrap), rather than the Solaneae (D'Arcy 1991). The Lycieae are circumscribed as in previous treatments and are represented here by one species of Grabowskia and five species of Lycium, which span the range of the distribution of the genus (N. America, S. America, Africa, Australia, Asia). Despite its broad distribution, relatively little cpDNA divergence is found within Lycium. The New World and Old World species each form a clade. The Jaboroseae here are restricted to two species of Jaborosa (one formerly assigned to the included genus Trechonaetes; Barboza & Hunziker 1987). Salpichroa (along with Nectouxia - not included in cpDNA study, but closely related to Salpichroa; A. Hunziker, pers. comm.) is reassigned to the Physaleae.

Another group of four tribes evident from this analysis (11 steps/85%), is the Physaleae, Capsiceae, Solaneae, and Datureae. The first three tribes comprise most of the traditional Solaneae and are a weakly supported (5 steps/15%) monophyletic group in Figures 5-6, but do not appear monophyletic in Figures 1-4. Previous cpDNA studies (Olmstead & Palmer 1992; Olmstead & Sweere 1994) also have found the Datureae to be included within the traditional Solaneae. Because the Datureae cannot be excluded with confidence from the branch defining the traditional Solaneae, and because the cpDNA results provide evidence identifying smaller monophyletic groups more consistent in size with other tribes, it is appropriate to provisionally split the Solaneae s.l. at this time.

The Solaneae here is more narrowly defined to include Solanum (with the included genera Cyphomandra and Lycopersicon), Jaltomata, and a few genera of uncertain relationship to Solanum (e.g., Discopodium, Normania, Triguera). The close relationship of Jaltomata to Solanum (Figs. 5-6) inferred from restriction site data (Olmstead & Palmer 1992; Mione & al. 1994) is not well supported by sequence data (e.g., Figs. 1-4 and Bohs & Olmstead, this volume), but the conclusion is complicated by the limited taxonomic sampling in the sequence data sets presently available. The most comprehensive data available (Figs. 5-6) show relatively weak support (23

steps/23%) for joining Jaltomata with Solanum. Further work may indicate that Jaltomata merits tribal distinction.

The tribe Capsiceae recognizes a group identified by the cpDNA data consisting of Capsicum and Lycianthes. A distinctive calyx morphology, shared by these two genera (D'Arcy 1986; Barboza & Hunziker 1992) provides further support for this group. These results suggest that Capsicum is derived from Lycianthes (Figs. 5-6), making Lycianthes paraphyletic, although this study represents limited sampling of both genera. Also, no members of the diverse Southeast Asian Lycianthes were included in this study, so the suggestion (D. Symon, pers. comm.) that they may not belong with the American species cannot be examined.

Tribe Physaleae has greater generic level diversity than any other tribe in the family, but has fewer total species than either the Solaneae or Capsiceae. Generic circumscriptions and relationships within this group are problematic and have been the subject of several studies (Averett 1979; Axelius & D'Arcy 1993; Mione et al. 1994; Ganapathi, this volume; Martinez, this volume; Estrada & Martinez, this volume; Zhang & Anmin, this volume; B. Axelius pers. comm.). The cpDNA results suggest a possible division of the Physaleae into four subtribes. The Salpichroinae consist of the two closely related genera Salpichroa and Nectouxia, formerly assigned to the Jaboroseae (D'Arcy 1991). The Iochrominae consist of five small genera restricted to South America, although the affinities of some genera provisionally assigned to subtribe Withaninae may lie with the Iochrominae. The representatives of the four genera in this study exhibit remarkably little cpDNA divergence (e.g., Dunalia australis and Vassobia lorentzii differ by a single restriction site character). Subtribe Withaninae is geographically more diverse, with Old World and New World members and may be too broadly circumscribed. Subtribe Physalinae is a complicated group of small satellite genera centered on the relatively large genus Physalis. Evidence presented here (Figs. 5-6) and elsewhere (Mione et al. 1994; Estrada & Martinez, this volume) indicates that several genera (e.g., Quincula, Margaranthus) are not distinct from Physalis and that generic boundaries within the group need to be redrawn. The paraphyletic arrangement of two species currently recognized as Witheringia at the base of the branch representing the Physalinae, suggests that this genus also might not be monophyletic.

The relationship of the remaining three small tribes, Solandreae, Mandragoreae, and Nicandreae, to each other and to the other tribes in the Solanoideae is not readily apparent. The Solandreae consist of the former monogeneric tribe Solandreae (as subtribe Solandrinae) and the traditional Juanulloeae (subtribe Juanulloinae), which are inferred to be sister groups on the basis of the limited sampling available in the cpDNA study. However, a cladistic analysis of this group based on morphology (Persson & al. 1994) suggests that Solandra is derived from within the Juanulloinae. If the latter relationship is confirmed, the subtribal divisions should be dropped. However, the substantial cpDNA difference between the representatives of the two subtribes argues against the conclusions of Persson & al. (1994). Mandragora is morphologically distinctive as well as being very divergent in its cpDNA and is recognized as a monogeneric tribe. The problem of placing an extremely divergent taxon in a molecular cladistic analysis (Felsenstein 1978) suggests that little can be said with regard to its relationship to other tribes. The two genera comprising the Nicandreae (Nicandra and Exodeconus) have a shared distribution in coastal Chile and Peru, which is consistent with a close phylogenetic relationship. Although the molecular evidence for grouping Nicandra

and Exodeconus is at best weak (26-35% bootstrap values and branch lengths of only 6-8 steps in Figs. 1-6) the molecular data do strongly oppose keeping Exodeconus in the Solaneae (sensu D'Arcy 1991). The suggestion that the relationship between Nicandra and Exodeconus indicates a past hybridization event possibly involving Nolana (Axelius 1994) is very unlikely given the highly divergent genomes of the three taxa.

A Comparison with the Classification of Hunziker, Barboza, Bernadello, and Cocucci

The provisional classification proposed here is contemporaneous with a revised classification for the family proposed by Hunziker & al. (this volume). At first glance, the differences between the two appear great, however, real conflicts between the two treatments are few. Hunziker & al. (this volume) recognize two subfamilies and 19 tribes, one with four subtribes, whereas this treatment recognizes 7 subfamilies and 20 tribal-level groups (including some subfamilies not divided into tribes), two of which are further divided into four and two subtribes. The two classifications are very similar with respect to circumscriptions of the Solanoideae and 11 tribes: Anthocercideae, Browallieae, Cestreae, Datureae, Hyoscyameae, Jaboroseae, Lycieae, Mandragoreae, Nicandreae, Nicotianeae (equals Petunieae here), and Salpiglossideae. Four of these tribes have only minor differences in circumscription: Jaboroseae (Salpichroa and Nectouxia removed to Physaleae), Hyoscyameae (here including Atropa), Nicandreae (here including Exodeconus), and Nicotianeae (here Nicotiana forms its own tribe and the rest of the traditional tribe plus Brunfelsia is referred to the Petunieae). Four groups differ only in rank: Schizanthoideae (here)/Schizantheae (Hunziker & al.), Schwenckioideae/Schwenckieae, Juanulloinae/Juanulloeae, and Solandrinae/ Solandreae. Table 2 identifies the differences between the two classifications. The placement of genera in this classification that are not included in the cpDNA studies have been made on the basis of traditional close relationships among genera; such decisions have been made with the generous assistance of many colleagues, including A. Hunziker and W. D'Arcy. A few poorly known genera are assigned to tribe with little confidence (indicated by "?" in Appendix 1).

The basis for the most prominent differences between the two classifications can be summarized by three points: 1) The adherence to phylogenetic principles in this classification results in the splitting of non-monophyletic groups, most notably the traditional subfamily Cestroideae. 2) Groups previously excluded from the family are included in this classification (e.g., Nolaneae, Goetzeoideae). 3) The traditional tribe Solaneae is split into several tribes and subtribes. The first point reflects a philosophical difference regarding the relationship of phylogeny to the construction of a classification. The latter two points reflect the new information now available from molecular studies with respect to family circumscription and relationships within the large and morphologically complicated Solaneae s.l. The strong congruence between these two classifications reflects the happy coincidence of inference based on traditional characters (e.g., morphology and anatomy) with inference based on cpDNA. The conflicts between these two classifications (e.g., the placement of Nicotiana, Exodeconus, Salpichroa) highlight groups in which further work is needed.

Acknowledgements

We wish to extend our deepest appreciation to the many individual researchers and Botanical Gardens who provided plant material for this study, most notably R. Lester and W. D'Arcy. We also wish to thank the many Solanaceae systematists who have provided thoughtful advice and commentary on issues pertaining to taxonomy and nomenclature in the family, including G. Anderson, G. Barboza, L. Bernadello, R. Bye, A. Child, A. Cocucci, W. D'Arcy, J. Hawkes, C. Heiser, A. Hunziker, S. Knapp, R. Lester, M. Martinez, T. Mione, M. Nee, R. Price, D. Spooner, and D. Symon.

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Figure captions.

Figure 1. Majority rule consensus tree, which is also one of the 12 equally most parsimonious trees from the first analysis (length = 3060; CI = 0.66). This analysis includes all 32 taxa for which sequences for one or both chloroplast genes are available. Restriction site data are included for 26 taxa. Proportional spacing is used and branch lengths are indicated. Branch lengths supporting infrafamilial groups identified in Fig. 2 are in bold type.

Figure 2. Strict consensus tree of 12 equally most parsimonious trees from the first analysis. Subfamilies of the provisional classification are indicated, as well as the X = 12 clade. Numbers indicate the percentage of bootstrap replicates supporting each clade. Dark bars indicate insertions (+) or deletions (-) in the ndhF sequence of ingroup members.

Figure 3. Majority rule consensus tree, which is also one of 8 equally most parsimonious trees from the second analysis (length = 2698; CI = 0.65). This analysis includes all taxa outside the "X=12" clade for which restriction site data are present (sequence data are included for five of these) and all taxa within the "X=12" clade for which both sequence and restriction site data are available. Proportional spacing is used and branch lengths are indicated. Branch lengths supporting infrafamilial groups identified in Fig. 4 are in bold type.

Figure 4. Strict consensus tree of 8 equally most parsimonious trees from the second analysis. Subfamilies of the provisional classification are indicated (representatives of Schwenckioideae and Goetzeoideae are not included), as well as tribes within subfamilies outside the X = 12 clade. Numbers indicate the percentage of bootstrap replicates supporting each clade.

Figure 5. Majority rule consensus tree, which is also one of 108 equally most parsimonious trees from the third analysis (length = 2245; CI = 0.58). This analysis includes 66 taxa within the "X=12" clade and 2 outgroup taxa in the Petunioideae. Restriction site data are available for all taxa and sequence data are available for 24 taxa. Proportional spacing is used and branch lengths are indicated. Branch lengths supporting tribes and subtribes identified in Fig. 6 are in bold type.

Figure 6. Strict consensus tree of 108 equally most parsimonious trees from the third analysis. Tribes and subtribes of the provisional classification for groups within the X = 12 clade are indicated. Numbers indicate the percentage of bootstrap replicates supporting each clade.

Fig 1

80
Mandragora
7
60
Juanulloa
9
36
Solandra
67
Capsicum baccatum
58
Solanum torvum
2
11
20
24
Cyphomandra betacea
32
8
43
Solanum tuberosum
29
40
Solanum lycopersicum
26
Jaltomata procumbens
3
11
63
Datura
9
17
Oryctes
47
13
Physalis alkekengi
25
51
Exodeconus
8
48
Nicandra
50
Atropa
37
48
Lycium cestroides
14
12
81
Jaborosa integrifolia
18
33
Nolana
67
Anthocercis
15
25
Nicotiana tabacum
12
22
25
Nicotiana acuminata
21
Petunia axillaris
35
18
Petunia parviflora
72
86
Nierembergia
15
69
31
Bouchetia
24
31
Hunzikeria
43
28
Browallia speciosa
141
54
Browallia eludens
31
64
Salpiglossis
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Goetzea
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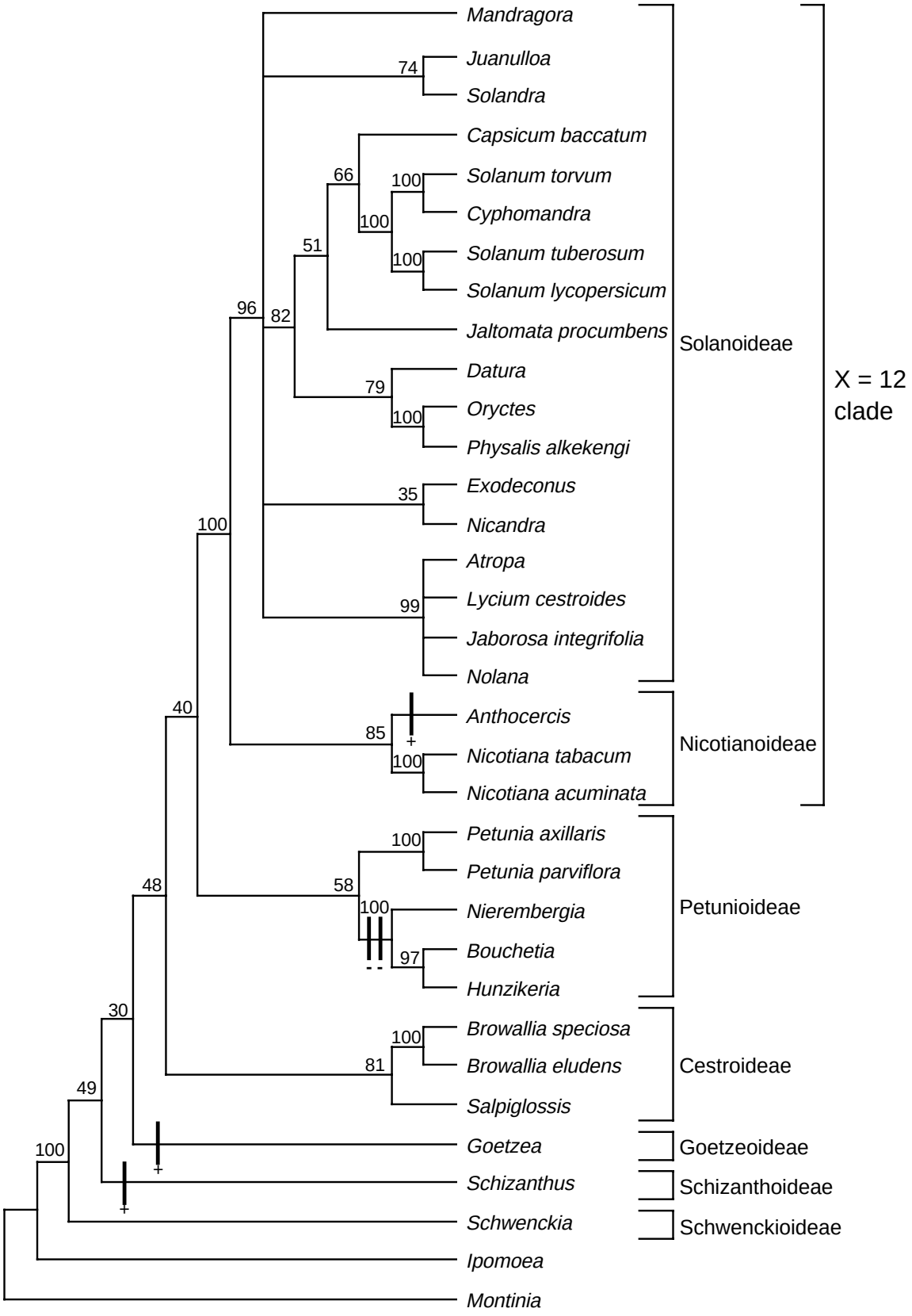
Schizanthus
76
Schwenckia
307
Ipomoea
190
Montinia

Fig. 2


Mandragora
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Solandra
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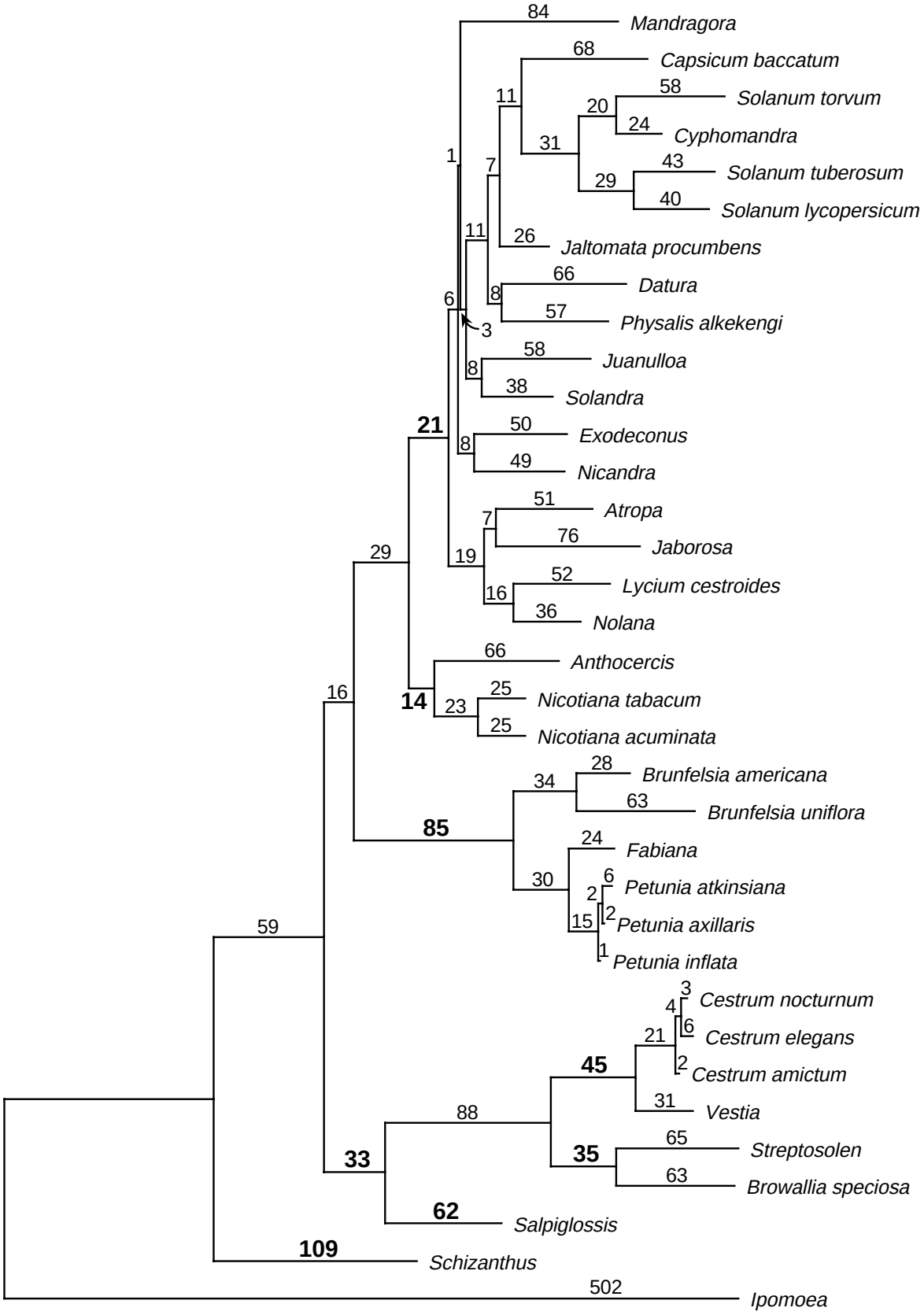
Solanum torvum
Cyphomandra
Solanum tuberosum
Solanum lycopersicum
Jaltomata procumbens
Datura
Oryctes
Physalis alkekengi
Exodeconus
Nicandra
Atropa
Lycium cestroides
Jaborosa integrifolia
Nolana
Anthocercis
Nicotiana tabacum
Nicotiana acuminata
Petunia axillaris
Petunia parviflora
Nierembergia
Bouchetia
Hunzikeria
Browallia speciosa
Browallia eludens
Salpiglossis
Goetzea
Schizanthus
Schwenckia
Ipomoea
Montinia
74
66
100
100
51
100
96
82
79
100
35
100
99
40
85
100
100
48
58
100
97
30
81
49
100
Solanoideae
Nicotianoideae
Petunioideae
Cestroideae
Goetzeoideae
Schizanthoideae
Schwenckioideae
X = 12
clade

Fig. 3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Mandragora
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Capsicum baccatum
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Cyphomandra
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7
43
Solanum tuberosum
29
40
Solanum lycopersicum
11
26
Jaltomata procumbens
66
Datura
6
8
57
Physalis alkekengi
3
58
Juanulloa
8
38
Solandra
21
50
Exodeconus
8
49
Nicandra
51
Atropa
7
76
Jaborosa
29
19
52
Lycium cestroides
16
36
Nolana
66
Anthocercis
16
14
25
Nicotiana tabacum
23
25
Nicotiana acuminata
28
Brunfelsia americana
34
63
Brunfelsia uniflora
85
24
Fabiana
30
6
Petunia atkinsiana
2
15
2
Petunia axillaris
1
Petunia inflata
59
3
Cestrum nocturnum
4
6
Cestrum elegans
21
45
2
Cestrum amictum
31
Vestia
88
65
Streptosolen
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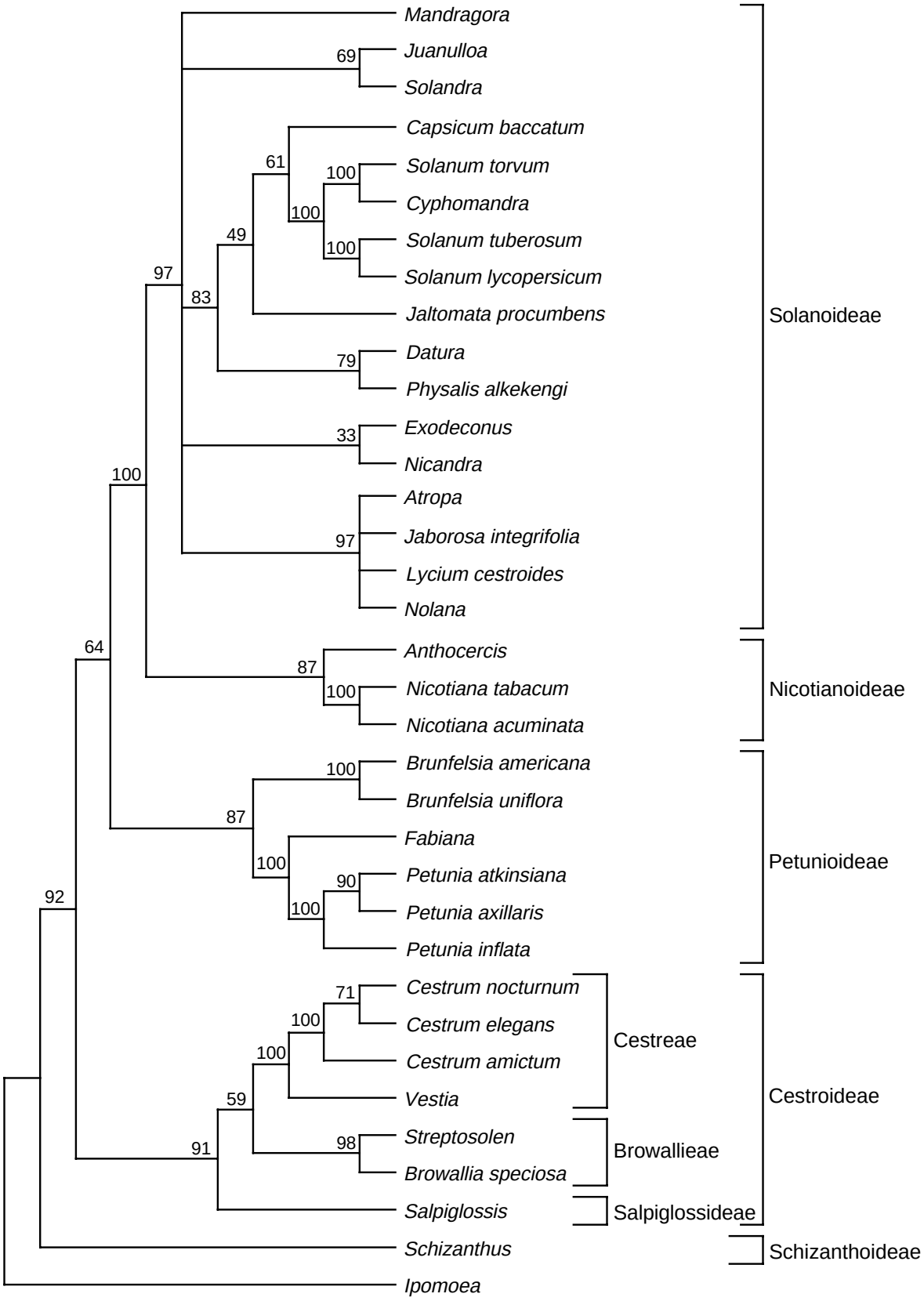
33
63
Browallia speciosa
62
Salpiglossis
109
Schizanthus
502
Ipomoea

Fig. 4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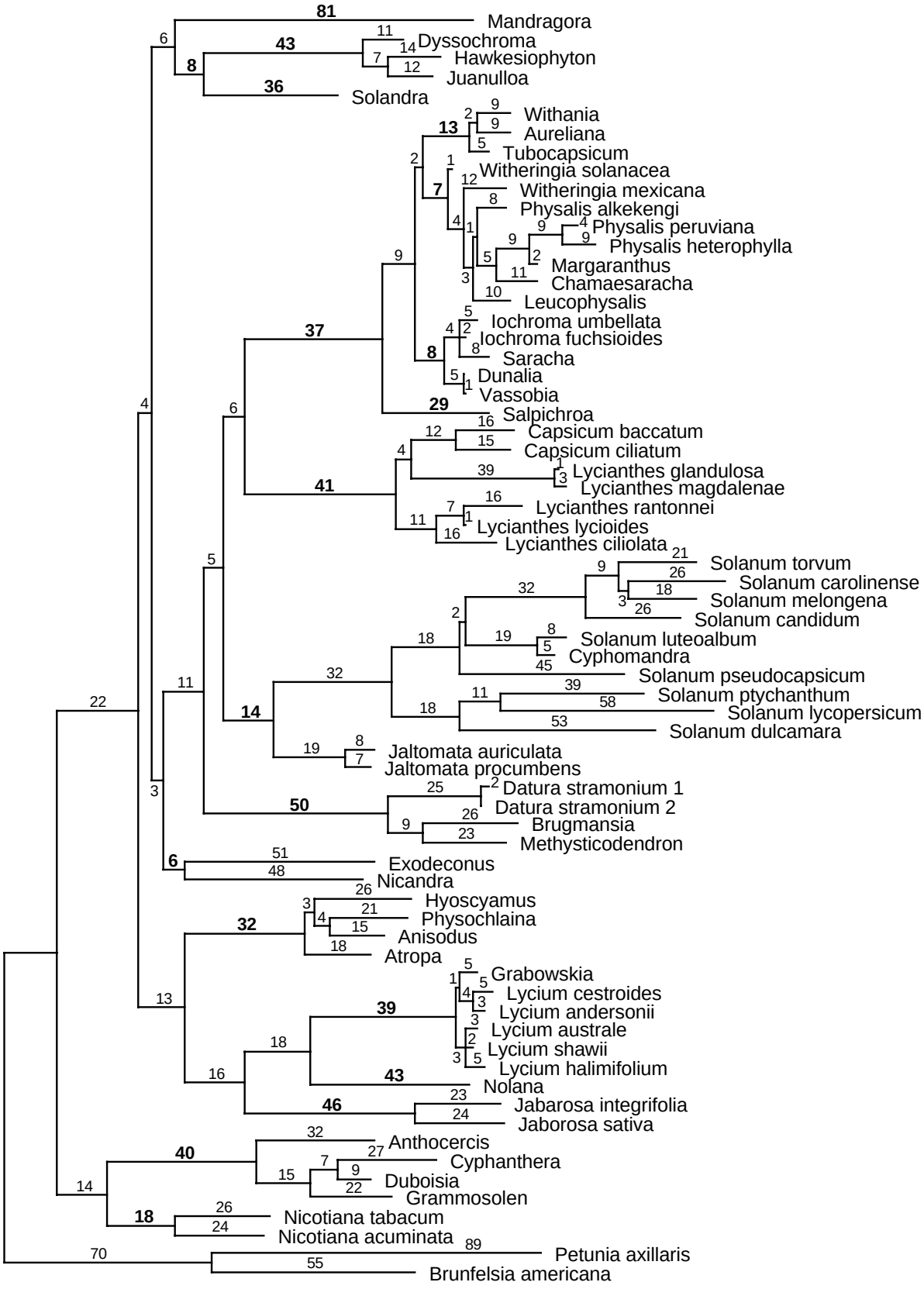
Datura
Physalis alkekengi
Exodeconus
Nicandra
Atropa
Jaborosa integrifolia
Lycium cestroides
Nolana
Anthocercis
Nicotiana tabacum
Nicotiana acuminata
Brunfelsia americana
Brunfelsia uniflora
Fabiana
Petunia atkinsiana
Petunia axillaris
Petunia inflata
Cestrum nocturnum
Cestrum elegans
Cestrum amictum
Vestia
Streptosolen
Browallia speciosa
Salpiglossis
Schizanthus
Ipomoea
69
61
100
100
100
49
97
83
79
33
100
97
64
87
100
100
87
100
90
100
92
71
100
100
59
98
91
Solanoideae
Nicotianoideae
Petunioideae
Cestroideae
Cestreae
Browallieae
Salpiglossideae
Schizanthoideae

Fig. 5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Hawkesiophyton
Juanulloa
Solandra
Withania
Aureliana
Tubocapsicum
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Witheringia mexicana
Physalis alkekengi
Physalis peruviana
Physalis heterophylla
Margaranthus
Chamaesaracha
Leucophysalis
Iochroma umbellata
Iochroma fuchsioides
Saracha
Dunalia
Vassobia
Salpichroa
Capsicum baccatum
Capsicum ciliatum
Lycianthes glandulosa
Lycianthes magdalenae
Lycianthes rantonnei
Lycianthes lycioides
Lycianthes ciliolata
Solanum torvum
Solanum carolinense
Solanum melongena
Solanum candidum
Solanum luteoalbum
Cyphomandra
Solanum pseudocapsicum
Solanum ptychanthum
Solanum lycopersicum
Solanum dulcamara
Jaltomata auriculata
Jaltomata procumbens
Datura stramonium 1
Datura stramonium 2
Brugmansia
Methysticodendron
Exodeconus
Nicandra
Hyoscyamus
Physochlaina
Anisodus
Atropa
Grabowskia
Lycium cestroides
Lycium andersonii
Lycium australe
Lycium shawii
Lycium halimifolium
Nolana
Jabarosa integrifolia
Jaborosa sativa
Anthocercis
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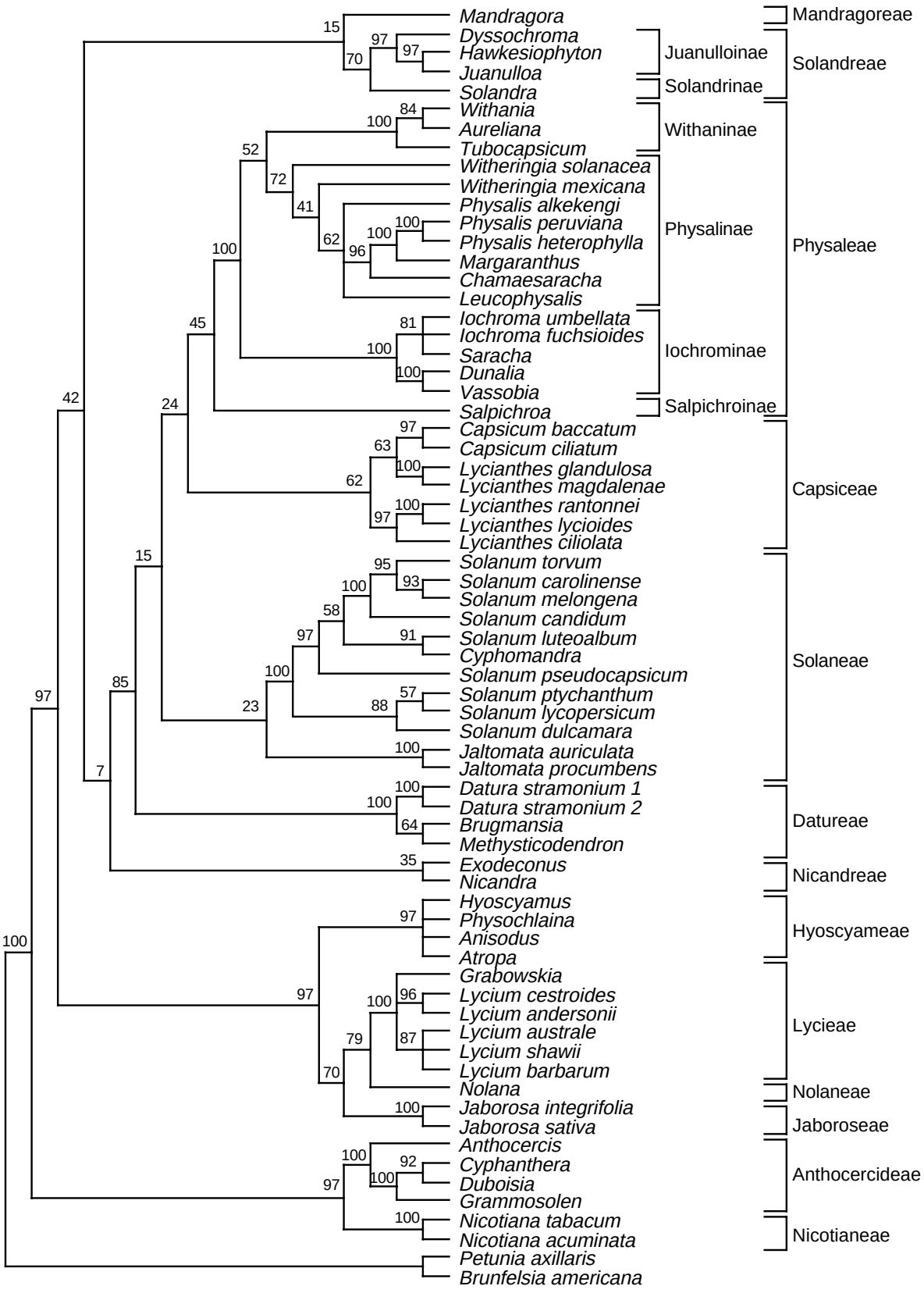
Grammosolen
Nicotiana tabacum
Nicotiana acuminata
Petunia axillaris
Brunfelsia americana

Fig. 6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Hawkesiophyton
Juanulloa
Solandra
Withania
Aureliana
Tubocapsicum
Witheringia solanacea
Witheringia mexicana
Physalis alkekengi
Physalis peruviana
Physalis heterophylla
Margaranthus
Chamaesaracha
Leucophysalis
Iochroma umbellata
Iochroma fuchsioides
Saracha
Dunalia
Vassobia
Salpichroa
Capsicum baccatum
Capsicum ciliatum
Lycianthes glandulosa
Lycianthes magdalenae
Lycianthes rantonnei
Lycianthes lycioides
Lycianthes ciliolata
Solanum torvum
Solanum carolinense
Solanum melongena
Solanum candidum
Solanum luteoalbum
Cyphomandra
Solanum pseudocapsicum
Solanum ptychanthum
Solanum lycopersicum
Solanum dulcamara
Jaltomata auriculata
Jaltomata procumbens
Datura stramonium 1
Datura stramonium 2
Brugmansia
Methysticodendron
Exodeconus
Nicandra
Hyoscyamus
Physochlaina
Anisodus
Atropa
Grabowskia
Lycium cestroides
Lycium andersonii
Lycium australe
Lycium shawii
Lycium barbarum
Nolana
Jaborosa integrifolia
Jaborosa sativa
Anthocercis
Cyphanthera
Duboisia
Grammosolen
Nicotiana tabacum
Nicotiana acuminata
Petunia axillaris
Brunfelsia americana
Juanulloinae
Solandrinae
Withaninae
Physalinae
Iochrominae
Salpichroinae
Mandragoreae
Solandreae
Physaleae
Capsiceae
Solaneae
Datureae
Nicandreae
Hyoscyameae
Lycieae
Nolaneae
Jaboroseae
Anthocercideae
Nicotianeae