

Olmstead, R.G., Sweere, J.A., Spangler, R.E., Bohs, L. & Palmer, J.D. (1999). Phylogeny and provisional classification of the Solanaceae based on chloroplast DNA. In: M. Nee, D.E. Symon, R.N. Lester & J.P. Jessop (editors). *Solanaceae IV*, pp. 111–137. Royal Botanic Gardens, Kew.

PHYLOGENY AND PROVISIONAL CLASSIFICATION OF THE SOLANACEAE BASED ON CHLOROPLAST DNA

RICHARD G. OLMSTEAD¹, JENNIFER A. SWEERE¹,
RUSSELL E. SPANGLER², LYNN BOHS³ & JEFFREY D. PALMER⁴

¹Department of E.P.O. Biology, University of Colorado, Boulder, CO 80309 U.S.A.
Current address: Olmstead, Department of Biology, Box 355325, University of Washington, Seattle, WA 98195-5325 U.S.A.; Sweere: Laboratory of Molecular Systematics, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 U.S.A.

²Department of E.P.O. Biology, University of Colorado, Boulder, CO 80309 U.S.A.
Current address: Harvard University Herbaria, 22 Divinity Ave., Cambridge MA 02138 U.S.A.

³Department of Biology, University of Utah, Salt Lake City, UT 84112 U.S.A.

⁴Department of Biology, Indiana University, Bloomington, IN 47405 U.S.A.

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 A. Hunziker, G. Barboza, L. Bernadello & A.A. Cocucci (in prep.).

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 et al. 1993a; Bremer et 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*, *Pauia*, *Sclerophyllax*, and *Tsoala*, whose affinities to the Solanaceae are debated (D'Arcy 1991; Hunziker et al., in prep.)

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 et al. 1987; Palmer 1991), its large yet manageable 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 et al. 1986) and has a total length, with subsequent corrections (Olmstead et 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 et al. 1988; Soltis et 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 et al. 1992, 1993a). Studies of cpDNA have clarified phylogenetic relationships in *Solanum* (Palmer & Zamir 1982; Hosaka et al. 1984; Spooner et al. 1993; Bohs & Olmstead, this volume; Bruneau et al. 1995; Bohs & Olmstead 1997 and Olmstead & Palmer 1997), *Nicotiana* (Kung et al. 1982; Olmstead & Palmer 1991), *Jaltomata* (Mione et al. 1994), and *Physalis* and related genera (Mione et al. 1994; Martínez, unpublished). 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, Salpiglossidae, 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).

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

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), Juanulloae (Persson et al. 1994), and Schwenckiae (D'Arcy & Benítez 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 (de Queiroz & Gauthier 1992) and the example set by Cantino et al. (1992). A comparison is made with the contemporary classification of Hunziker et al. (in prep.).

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 sub-unit of the photosynthesis enzyme rubisco) and *ndhF* (encoding a sub-unit of the chloroplast NADH dehydrogenase). Data acquisition and analysis for each method are detailed elsewhere (restriction sites – Olmstead & Palmer 1992; sequencing – Olmstead et 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 et al. 1993a; Olmstead & Sweere 1994; Olmstead & Reeves 1995; Scotland et 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, 1997). 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* Van Devender & Jenkins, for which this is the only source of data. Two out-group 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 site 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; 1997). 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

TABLE 1. Accessions used in cpDNA analyses. Type of data, restriction sites (RFLP), *rbcL* sequences or *ndhF* sequences, is indicated.

Species	Source ¹	Voucher ²	RFLP	rbcL	ndhF
Solanaceae:					
<i>Anisodus luridus</i> Link	BIRM S.0215	BIRM	X		
<i>Anthocercis viscosa</i> R. Br.	Australia	Symon 14835 AD	X	X	X
<i>Aureliana fasciculata</i> (Sendt.) Barb. & A. Hunz.	Brazil	Brown s.n. IAC	X		
<i>Atropa belladonna</i> L.	BIRM S.0078	BIRM	X	X	X
<i>Bouchetia erecta</i> Dun.	Missouri Bot. Gard.	D'Arcy 17791 MO		X	X
<i>Browallia speciosa</i> Hook.	BIRM S.0416	Olmstead S-6 WTU	X	X	X
<i>Browallia eludens</i> Van Devender & Jenkins	Arizona, USA	P. Jenkins & al. 90-106 WTU			X
<i>Brugmansia sanguinea</i> (Ruiz & Pav.) D. Don	Bogota Jard. Bot.	Olmstead S-7 WTU	X		
<i>Brunfelsia americana</i> L.	Matthaei Bot. Gard.	#840215	X		
<i>Brunfelsia uniflora</i> (Pohl) D. Don	Brazil	Brown s.n. IAC	X		
<i>Capsicum baccatum</i> L.	Bolivia	Eshbaugh 1584 MU	X	X	X
<i>Capsicum ciliatum</i> (H.B.K.) O. Kuntze	Ecuador	C. Heiser 7518 MU	X		
<i>Cestrum amictum</i> (Sendt.) Dunal	Brazil	Brown s.n. IAC	X		
<i>Cestrum elegans</i> (Brongniart) Schltdl.	Bogota Jard. Bot.	Olmstead S-9 WTU	X		
<i>Cestrum nocturnum</i> L.	Matthaei Bot. Gard.	#21314	X		
<i>Chamaesaracha coronopus</i> (Dunal) Gray	Texas, USA	Turner 15854 TEX	X		
<i>Cyphanthera anthocercidea</i> (F. Muell.) Haegi	Australia	Symon 14836 AD	X		
<i>Cyphomandra betacea</i> (Cav.) Sendt.	Bolivia	Bohs 2468 UT	X		X
<i>Datura stramonium</i> L. 1	Michigan, USA	Olmstead S-16 WTU	X	X	X
<i>Datura stramonium</i> L. 2	Beal Bot. Gard.	Olmstead S-14 WTU	X		
<i>Duboisia myoporoides</i> R. Br.	Australia	Symon 14832 AD	X		
<i>Dunalia australis</i> (Griseb.) Sleumer	BIRM S.0379	Olmstead S-17 WTU	X		
<i>Dysochroma viridiflora</i> (Sims) Miers	Brazil	Brown s.n. IAC	X		
<i>Exodeconus miersii</i> (Hook.) D'Arcy	BIRM S.1223	BIRM	X	X	X
<i>Fabiana imbricata</i> Ruiz & Pav.	UCSB Bot. Gard.	#81342	X		
<i>Goetzea elegans</i> Wydler	Waimea Arboretum	#87S381		X	X
<i>Grabowskia duplicata</i> Arnott	BIRM S.0258	BIRM	X		
<i>Grammosolen dixonii</i> (F. Muell. & R. Tate) Haegi	Australia	Symon 14833 AD	X		

TABLE 1. cont.

Species	Source ¹	Voucher ²	RFLP	rbcL	ndhF
<i>Hawkesiophyton panamensis</i> (Standley) A. Hunz.	BIRM S.1462	BIRM	X		
<i>Hunzikeria texana</i> (Torrey) D'Arcy	Texas, USA	<i>C. Ferguson 089</i> TEX		X	X
<i>Hyoscyamus albus</i> L.	BIRM S.1218	<i>Olmstead S-25</i> WTU	X		
<i>Iochroma fuchsoides</i> Miers	Bogota Jard. Bot.	<i>Olmstead S-29</i> WTU	X		
<i>Iochroma umbellata</i> (Ruiz & Pav.) A. Hunz.	UCB Bot. Gard. #65.0948	<i>P.C. Hutchison et al. 6240</i> UC	X		
<i>Jaborosa integrifolia</i> Lam.	BIRM S.0290	BIRM	X	X	X
<i>Jaborosa sativa</i> (Miers) Barb. & A. Hunz. (syn. <i>Trechonaetes sativa</i> Miers)	BIRM S.0234	BIRM	X		
<i>Jaltomata auriculata</i> ³ (= <i>Saracha auriculata</i> Miers)	BIRM S.1596	<i>Olmstead S-23</i> WTU	X		
<i>Jaltomata procumbens</i> (Cav.) J. Gentry	Beal Bot. Gard.	<i>Olmstead S-24</i> WTU	X		X ⁴
<i>Juanulloa mexicana</i> (Schltdl.) Miers	BIRM S.0411	BIRM	X	X	X
<i>Leucophysalis grandiflora</i> (Hook.) Rydb.	Michigan, USA	<i>Olmstead S-30</i> WTU	X		
<i>Lycianthes ciliolata</i> (Mart. & Gal.) Bitt.	BIRM S.0607	BIRM	X		
<i>Lycianthes glandulosa</i> Bitt.	BIRM S.1616	BIRM	X		
<i>Lycianthes lycioides</i> (L.) Hassl.	Bogota Jard. Bot.	<i>Olmstead S-87</i> WTU	X		
<i>Lycianthes rantonnei</i> (Carr.) Hassl.	BIRM S.0928	<i>Olmstead S-96</i> WTU	X		
<i>Lycianthes magdalenae</i> Bitt.	Colombia	<i>Olmstead S-32</i> WTU	X		
<i>Lycium andersonii</i> Gray	BIRM S.1480	BIRM	X		
<i>Lycium australe</i> F. Muell.	Australia	<i>Symon 14834</i> AD	X		
<i>Lycium cestroides</i> Schltdl.	BIRM S.0368	<i>Olmstead S-34</i> WTU	X	X	X
<i>Lycium barbarum</i> L.	Michigan, USA (cult)	<i>Olmstead S-35</i> WTU	X		
<i>Lycium shawii</i> Roem. & Schult.	BIRM S.1194	<i>Olmstead S-36</i> WTU	X		
<i>Mandragora officinarum</i> L.	BIRM S.0672	BIRM	X	X	X
<i>Margaranthus solanaceus</i> Schltdl.	BIRM S.0610	<i>Olmstead S-37</i> WTU	X		
<i>Methysticodendron amesianum</i> Schultes (= <i>Brugmansia candida</i> Pers.)	BIRM S.0412	BIRM	X		
<i>Nicandra physalodes</i> (L.) Gaertn.	Beal Bot. Gard.	<i>Olmstead S-38</i> WTU	X	X	X
<i>Nicotiana acuminata</i> Hook.	BIRM S.0372	<i>Olmstead S-39</i> WTU	X	X ⁵	X
<i>Nicotiana tabacum</i> L.	Matthaei Bot. Gard.	no voucher	X	X ⁶	X
<i>Nierembergia hippomanica</i> Miers	Beal Bot. Gard.	<i>Olmstead S-58</i> WTU		X	X

TABLE 1 cont.

Species	Source ¹	Voucher ²	RFLP rbcL ndhF		
<i>Nolana spathulata</i> Ruiz & Pav.	Peru	<i>Dillon & Dillon 3767 F</i>	X	X	X
<i>Oryctes nevadensis</i> S. Watson	Nevada, USA	<i>A. Tiehm 11982 WTU</i>		X	X
<i>Petunia atkinsiana</i> D. Don ex Loud.	BIRM S.0640	<i>Olmstead S-61 WTU</i>	X		
<i>Petunia axillaris</i> (Lam.) B.S.P.	BIRM S.0367	<i>Olmstead S-60 WTU</i>	X	X ⁷	X
<i>Petunia inflata</i> R.E. Fries	BIRM S.0172	<i>Olmstead S-62 WTU</i>	X		
<i>Petunia parviflora</i> Juss.	Arizona, USA	<i>A.C. Sanders 5835 WTU</i>		X	X
<i>Physalis alkekengi</i> L.	Missouri Bot. Gard.	<i>D'Arcy 17707 MO</i>	X	X	X
<i>Physalis heterophylla</i> Nees	Michigan, USA	<i>Olmstead S-64 WTU</i>	X		
<i>Physalis peruviana</i> L.	Bogota Jard. Bot.	<i>Olmstead S-69 WTU</i>	X		
<i>Physochlaina orientalis</i> G. Don	BIRM S.0125	BIRM	X		
<i>Saracha spinosa</i> (Dammer) D'Arcy & Smith	UCB Bot. Gard. #75.0784	<i>Plouman 4651 UC</i>	X		
<i>Salpichroa origanifolia</i> (Lam.) Baillon	BIRM S.0291	<i>Olmstead S-70 WTU</i>	X		
<i>Salpiglossis sinuata</i> Ruiz & Pav.	BIRM S.0181	<i>Olmstead S-71 WTU</i>	X	X	X
<i>Schizanthus pinnatus</i> Ruiz & Pav.	BIRM S.0224	<i>Olmstead S-72 WTU</i>	X	X	X
<i>Schwenckia lateriflora</i> (Vahl) Carvalho	Venezuela	<i>Benítez de Rojas 3901 MO</i>		X	X
<i>Solandra grandiflora</i> Swartz	Matthaei Bot. Gard.	#840415	X	X	X
<i>Solanum candidum</i> Lindl.	BIRM S.0975	<i>Olmstead S-100 WTU</i>	X		
<i>Solanum carolinense</i> L.	BIRM S.1816	<i>Olmstead S-77 WTU</i>	X		
<i>Solanum dulcamara</i> L.	Michigan, USA	no voucher	X		X
<i>Solanum luteoalbum</i> Pers.	Peru	<i>Hawkes S42 BIRM</i>	X		
<i>Solanum lycopersicum</i> L.	Michigan, USA (cult)	no voucher	X	X	X
<i>Solanum melongena</i> L.	BIRM S.0657	<i>Olmstead S-91 WTU</i>	X		
<i>Solanum pseudocapsicum</i> L.	BIRM S.0870	BIRM	X		
<i>Solanum ptychanthum</i> Dunal	Illinois, USA	<i>Olmstead S-94 WTU</i>	X		X
<i>Solanum torvum</i> Swartz	BIRM S.0839	<i>Olmstead S-101 WTU</i>	X		X
<i>Solanum tuberosum</i> L.	USDA ARS	#1610	X	X	X
<i>Streptosolen jamesonii</i> Miers	Bogota Jard. Bot.	<i>Olmstead S-106 WTU</i>	X		
<i>Tubocapsicum anomalum</i> (Franchet & Savat.) Makino	Missouri Bot. Gard.	<i>Chen 231 MO</i>	X		
<i>Vassobia lorentzii</i> (Dammer) A. Hunz.	BIRM S.0376	BIRM	X		
<i>Vestia foetida</i> (Ruiz & Pav.) Hoffmannsegg	BIRM S.0105	BIRM	X		

TABLE 1 cont.

Species	Source ¹	Voucher ²	RFLP rbcL ndhF		
<i>Withania coagulans</i> (Stocks) Dunal	BIRM S.0678	<i>Olmstead S-109</i> WTU	X		
<i>Witheringia mexicana</i> (Robinson) A. Hunz.	BIRM S.1199	BIRM	X		
<i>Witheringia solanacea</i> L'Hérit.	Missouri Bot. Gard.	<i>D'Arcy 16399</i> MO	X		
Convolvulaceae:					
<i>Calonyction aculeatum</i> House (= <i>Ipomoea bona-nox</i> L.)	Beal Bot. Gard.	no voucher	X		
<i>Ipomoea coccinea</i> L.	Beal Bot. Gard.	<i>Olmstead 88-015</i> WTU	X	X	X
Montiniaceae:					
<i>Montinia caryophyllacea</i> Thunb.	DNA from D. Soltis	<i>Williams 2833</i> MO		X	X
Totals: 92			83	30	36

¹ Sources of plant material: Beal Bot. Gard. – Michigan State University, East Lansing, Michigan, USA; BIRM – University of Birmingham Solanaceae seed collection, Birmingham, England; Bogota Jard. Bot. – Bogota Botanic Garden, Bogota, Colombia; Missouri Bot. Gard. – Missouri Botanical Garden, St. Louis, Missouri, USA; UCB Bot. Gard. – University of California, Berkeley, California, USA; UCSB Bot. Gard. – University of California, Santa Barbara, California, USA; USDA ARS – United States Department of Agriculture, Agriculture Research Station, Madison, Wisconsin, USA; Waimea Arboretum – Waimea, Hawaii, USA; all others wild collected or collected from uncultivated cultivation “(cult)”.

² Herbarium vouchers as indicated or accession numbers for Botanical Garden collections.

³ This combination is suggested in Mione et al. 1994.

⁴ Accession for *ndhF* sequence (voucher: *Davis 1189A* CONN) different from one used for restriction site study

⁵ *rbcL* sequence of *N. acuminata* determined by Lin et al. 1986 from different accession from that used here for RFLP and *ndhF* data

⁶ *rbcL* sequence of *N. tabacum* determined by Lin et al. 1986 from different accession from that used here for RFLP and *ndhF* data

⁷ *rbcL* sequence is that of *P. hybrida* determined by Aldrich et al. 1986

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 out-group, *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 (de Queiroz & 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 out-groups, 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 & 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

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

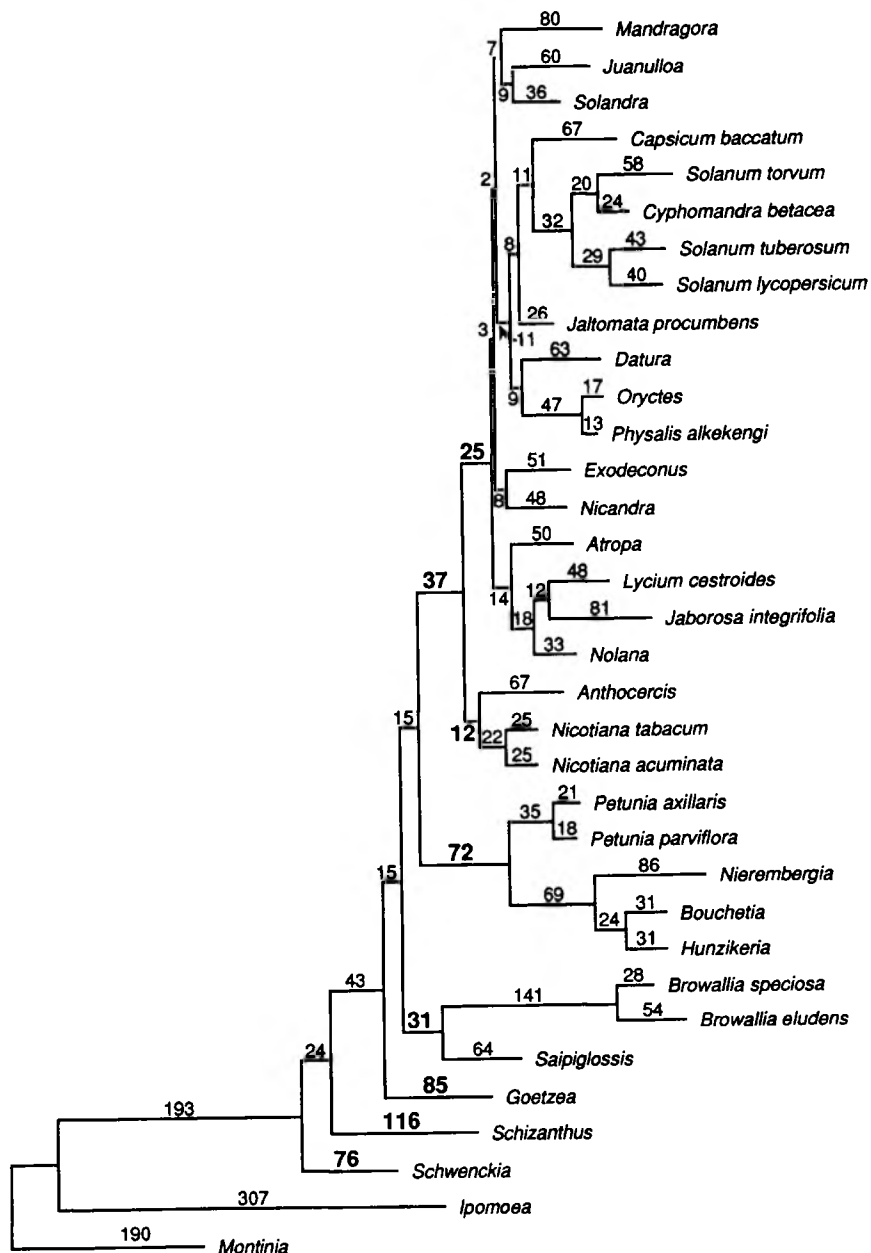


FIG. 1. Majority rule consensus tree, which is also one of the 12 equally most parsimonious trees from the first analysis (length = 3060; CI = 0.66). This analysis includes all 32 taxa for which sequences for one or both chloroplast genes are available. Restriction site data are included for 26 taxa.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

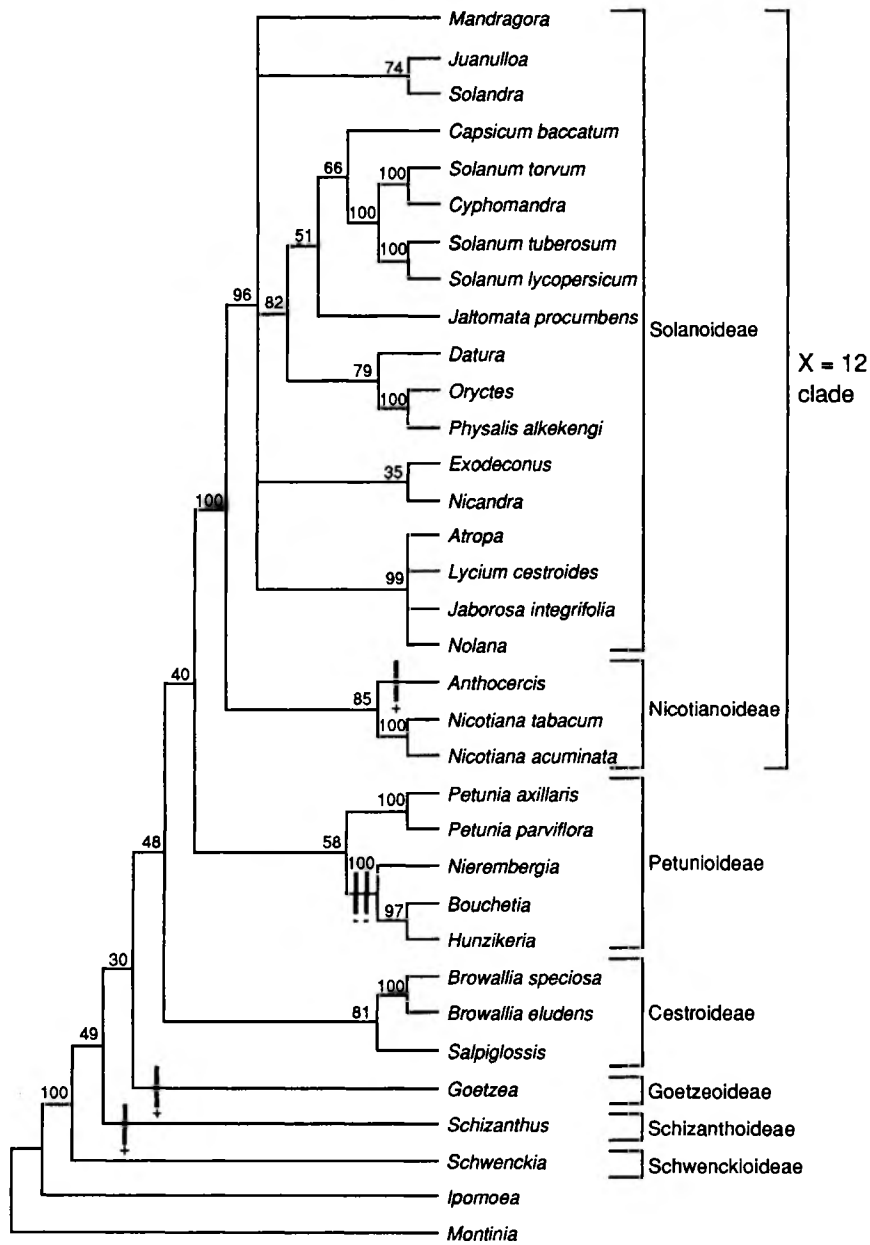


FIG. 2. Strict consensus tree of 12 equally most parsimonious trees from the first analysis. Subfamilies of the provisional classification are indicated, as well as the "X = 12" clade. Numbers indicate the percentage of bootstrap replicates supporting each clade. Dark bars indicate insertions (+) or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

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

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 out-group *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 out-group 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 Jaboroseae, 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, Hunziker 1995) 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). 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

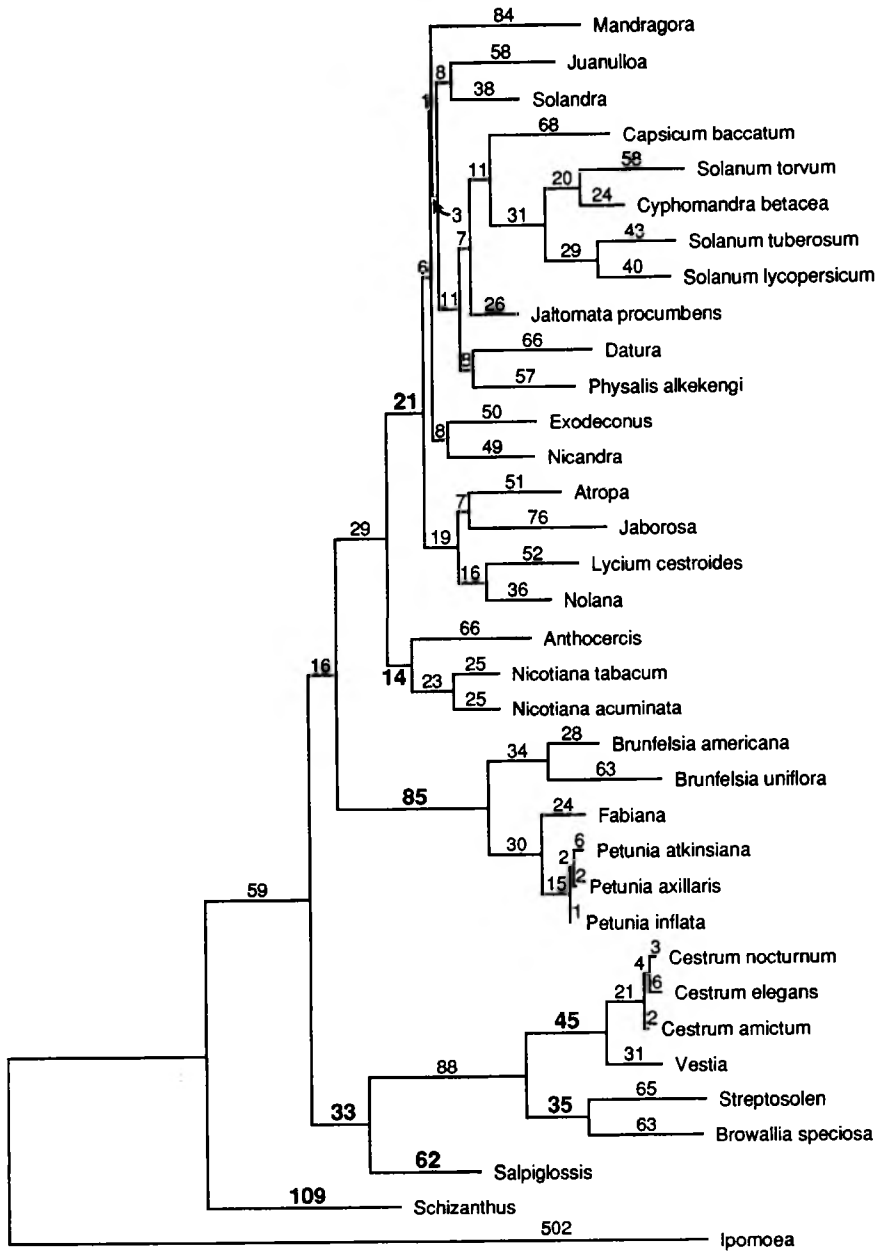


FIG. 3. Majority rule consensus tree, which is also one of 8 equally most parsimonious trees from the second analysis (length = 2698; CI = 0.65). This analysis includes all taxa outside the "X=12" clade for which restriction site data are present (sequence data are included for five of these) and all 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.

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

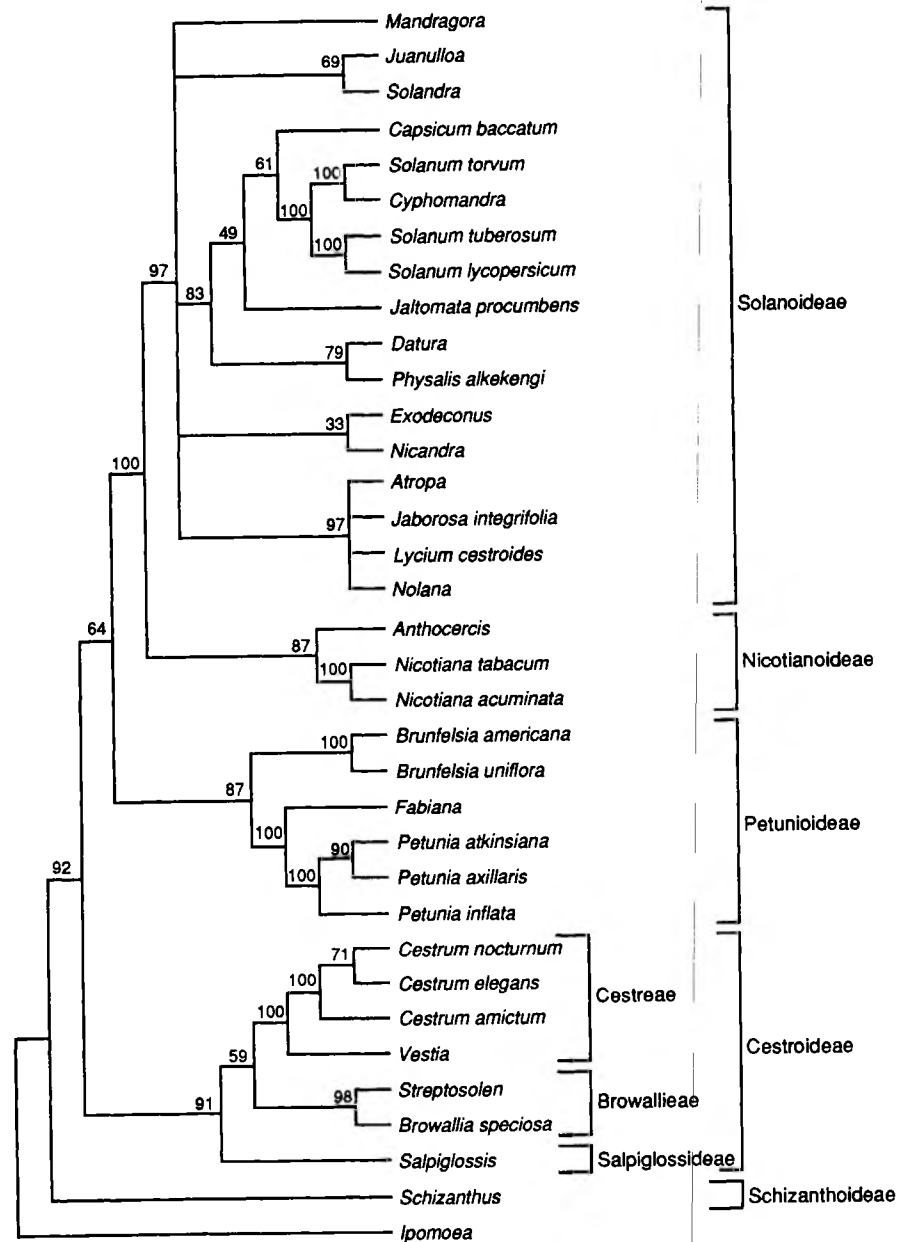


FIG. 4. Strict consensus tree of 8 equally most parsimonious trees from the second analysis. Subfamilies of the provisional classification are indicated (representatives of Schwenkioideae and Goetzieoideae are not included), as well as tribes within subfamilies outside the "X = 12" clade. Numbers indicate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

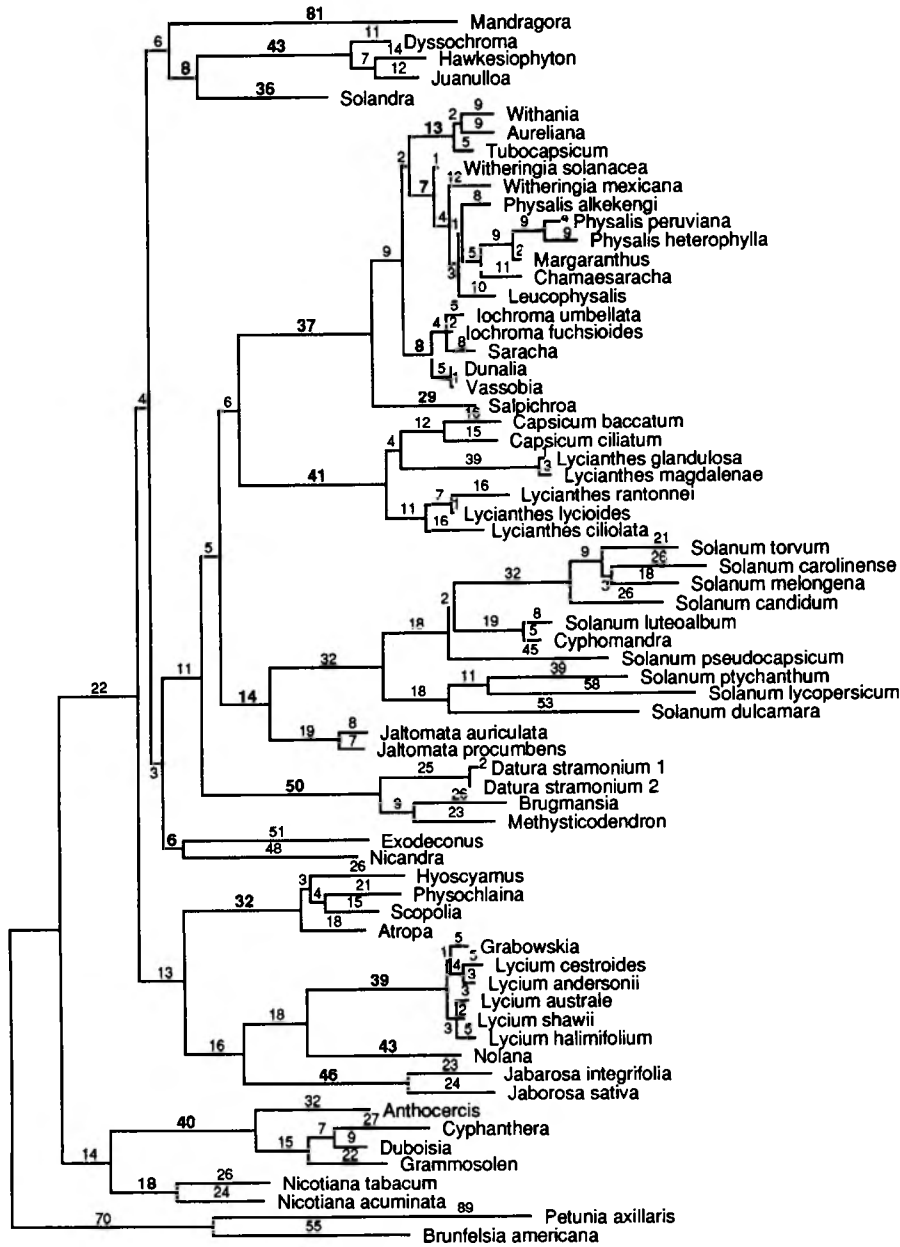


FIG. 5. Majority rule consensus tree, which is also one of 108 equally most parsimonious trees from the third analysis (length = 2245; CI = 0.58). This analysis includes 66 taxa within the "X = 12" clade and 2 out-group taxa in the Petunioidae. Restriction site data are available for all taxa and sequence 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.

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

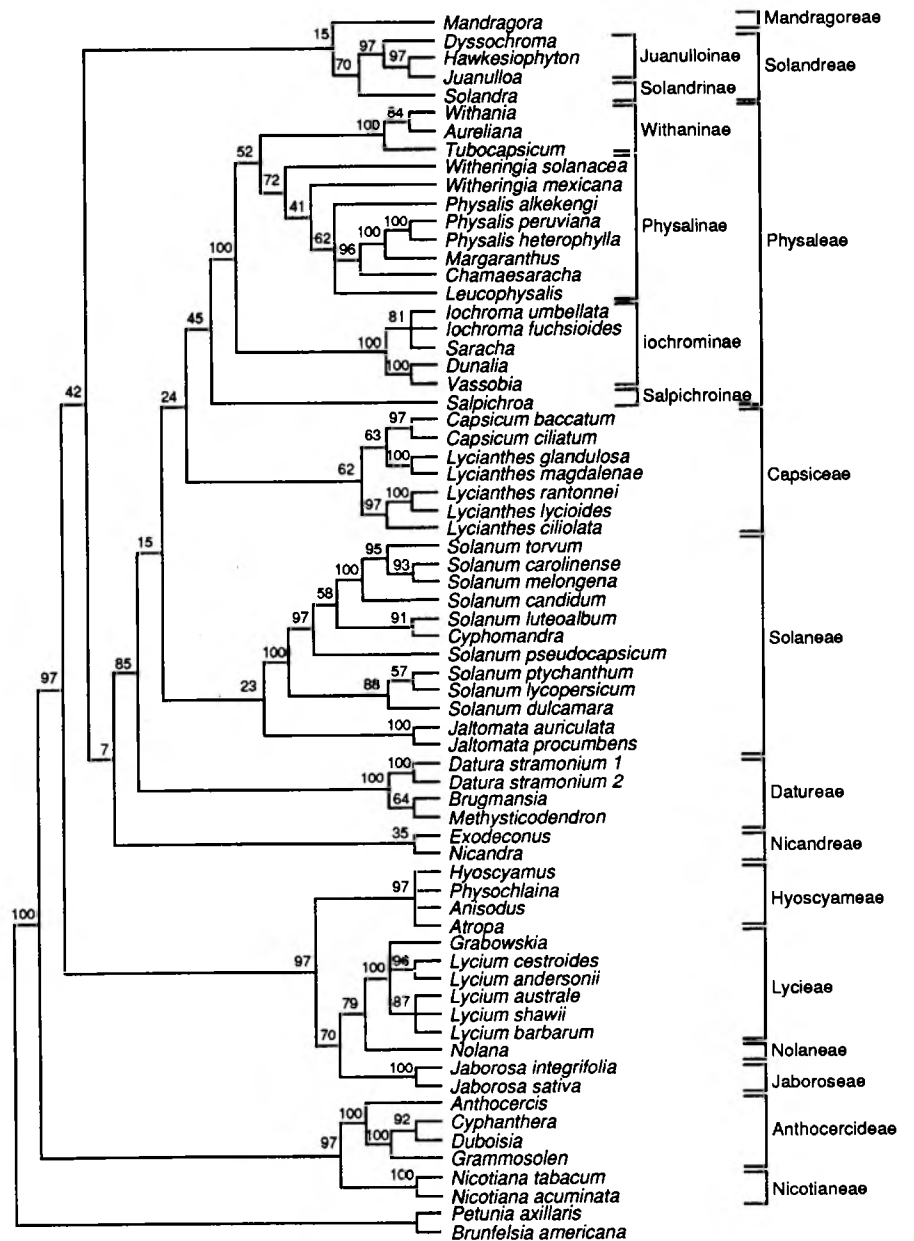


FIG. 6. Strict consensus tree of 108 equally most parsimonious trees from the third analysis. Tribes and subtribes of the provisional classification for groups within the "X = 12" clade are indicated. Numbers indicate the percentage of bootstrap replicates supporting each clade.

Cyphomandra) and *Jaltomata*, a new tribe Capsiceae (D'Arcy & Averett 1996), represented here by *Capsicum* and New World species of *Lycianthes*, and a new large tribe Physaleae (Miers 1849), 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* (Datoreae), 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 (de Queiroz & 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.

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

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 (Hunziker 1995), 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 pers. comm.) and limited taxonomic sampling of sequences for the nuclear gene *rbcS* (Meagher et 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 et 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; Sudhkaran & Ganapathi, this volume; Martínez, unpublished; Estrada & Martínez, this volume; Zhang & Lu, 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 & Martínez, 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 Juanulloae (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 et 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 et 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 Solanae (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 and colleagues (in prep.). At first glance, the differences between the two appear great, however, real conflicts between the two treatments are few. Hunziker (pers comm.) would 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)/Schizanthaceae (sensu Hunziker), Schwenckioideae/Schwenckieae, Juanulloinae/Juanulloae, 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).

TABLE 2. Differences between classifications of Hunziker et al. (pers. comm.) and Olmstead et al (Appendix 1). Differences that are due to inclusion of taxa in this classification only, acceptance of paraphyletic groups by Hunziker et al. (pers. comm.), or splitting in one classification vs. the other are not regarded as in conflict. Differences that indicate the existence of a putatively polyphyletic group in one classification or the other are regarded as in conflict. Differences are arranged in order of increasing significance.

Taxon	Hunziker et al.	Olmstead et al.	Basis for Difference
Solaneae	single tribe (28 genera)	3 tribes: Capsiceae (2 genera) Physaleae (ca. 20 genera), 4 subtribes Solaneae (ca. 8 genera)	Splitting
<i>Atropa</i>	Atropeae	Hyoscyameae	Splitting; possibly Paraphyly/Monophyly
<i>Latua</i>	Latueae	Petunioideae	Splitting; possibly Paraphyly/Monophyly
<i>Brunfelsia</i>	Francisceae	Petunioideae	Splitting; possibly Paraphyly/Monophyly
Cestroideae	single paraphyletic subfamily	5 monophyletic subfamilies	Paraphyly/Monophyly
<i>Nolana</i>	not included	Nolaneae, subfam. Solanoideae	Excluded from Hunziker et al.
<i>Goetzea</i>	not included	Goetzeoideae	Excluded from Hunziker et al.
<i>Exodeconus</i>	Solaneae	Nicandreae	Polyphyly/Monophyly
<i>Salpichroa, Nectouxia</i>	Jaboroseae	Physaleae subtr. Salpichroinae	Polyphyly/Monophyly
<i>Nicotiana</i>	Nicotianeae subtr. Nicotianineae, with <i>Petunia</i> & <i>Fabiana</i>	Nicotianeae, by itself	Polyphyly/Monophyly

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

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. Martínez, T. Mione, M. Nee, R. Price, D. Spooner, and D. Symon.

References

- Armstrong, J.E. 1986. Comparative floral anatomy of Solanaceae: a preliminary survey. In W.G. D'Arcy (ed.), *Solanaceae: Biology and Systematics*, pp. 101–113. Columbia Univ. Press, New York.
- Averett, J.E. 1979. Biosystematics of the physaloid genera of the Solaneae in North America. In J.G. Hawkes, R.N. Lester, & A.D. Skelding (eds.), *The Biology and Taxonomy of the Solanaceae*, pp. 493–504. Academic Press, London.
- Axelius, B. 1994. The genus *Exodeconus* and some comments on its relation with *Nicandra* (Solanaceae). *Pl. Syst. Evol.* 193: 153–172.
- Axelius, B. & D'Arcy, W.G. 1993. A new species of *Deprea* (Solanaceae) from Venezuela. *Novon* 3: 11–13.
- Barboza, G.E. & Hunziker, A.T. 1987. Estudios sobre Solanaceae XXV. Revisión de *Jaborosa*. *Kurtziana* 19: 77–153.
- Barboza, G.E. & Hunziker, A.T. 1992. Estudios sobre Solanaceae XXXIII. El género *Lycianthes* in La Argentina. *Darwiniana* 31: 17–34.
- Bentham, G. 1876. Solanaceae. In G. Bentham and J.D. Hooker (eds.), *Genera Plantarum* 2(1): 882–913. L. Reeve & Co., London.
- Bohs, L. & Olmstead, R.G. 1995. *Solanum* phylogeny inferred from chloroplast DNA sequence data. In *Solanaceae IV, Advances in Biology and Utilization*, M. Nee, D.E. Symon, J.P. Jessop and J.G. Hawkes, eds. Royal Botanic Gardens, Kew, this volume.
- Bohs, L. & Olmstead, R.G. 1997. Phylogeny of *Solanum* (Solanaceae) subgenera based on *ndhF* sequence data. *Syst. Bot.* 22: 5–17.
- Bremer, K. & Jansen, R.K. 1992. A new subfamily of the Asteraceae. *Ann. Missouri Bot. Gard.* 79: 414–415.
- Bremer, B., Olmstead, R.G., Struwe, L., & Sweere, J.A. 1994. *rbcL* sequences support exclusion of *Retzia*, *Desfontainia*, and *Nicodemia* from the Gentianales. *Pl. Syst. Evol.* 190: 213–230.

- Bruneau, A., Dickson, E.E. & Knap, S. 1995. Congruence of chloroplast DNA restriction site characters with morphological and isozyme data in *Solanum* sect. *Lasiocarpa*. *Can. J. Bot.* 73: 1151–1167.
- Cantino, P.D., Harley, R.M., & Wagstaff, S.J. 1992. Genera of Labiatae: status and classification. In R. Harley (ed.), *Advances in Labiate Science*, pp. 511–522. Royal Botanic Gardens, Kew.
- Carlquist, S. 1987. Wood anatomy of Nolanaceae. *Aliso* 11: 463–471.
- Clegg, M.T. 1993. Chloroplast gene sequences and the study of plant evolution. *Proceedings of the National Academy of Sciences, U.S.A.* 90: 363–367.
- D'Arcy, W.G. 1979. The classification of the Solanaceae. In J.G. Hawkes, R.N. Lester, & A.D. Skelding (eds.), *The Biology and Taxonomy of the Solanaceae*, pp. 3–48. Academic Press, London.
- D'Arcy, W.G. 1986. The calyx in *Lycianthes* and some other genera. *Ann. Missouri Bot. Gard.* 73: 117–127.
- D'Arcy, W.G. 1991. The Solanaceae since 1976, with a review of its biogeography. In J.G. Hawkes, R.N. Lester, M. Nee, & N. Estrada-R. (eds.), *Solanaceae III: Taxonomy, Chemistry, Evolution*, pp. 75–138. Royal Botanic Garden, Kew.
- D'Arcy, W.G. & Averett, J.E. 1996. Recognition of tribes Capsiceae and Physaleae, subfamily Solanoideae, Solanaceae. *Phytologia* 80: 273–275.
- D'Arcy, W.G. & Benítez de Rojas, C. 1991. Biogeographical mapping: the Schwenckieae example. In J.G. Hawkes, R.N. Lester, M. Nee, & N. Estrada-R. (eds.), *Solanaceae III: Taxonomy, Chemistry, Evolution*, pp. 169–179. Royal Botanic Garden, Kew.
- Darwin, C. 1859. *The Origin of Species*. John Murray, London.
- de Queiroz, K. & Gauthier, J. 1992. Phylogenetic taxonomy. *Ann. Rev. Ecol. Syst.* 23: 449–480.
- Doyle, J.J. 1993. DNA, phylogeny, and the flowering of plant systematics. *BioScience* 43: 380–389.
- Estrada, E. & Martínez, M. 1995. *Physalis* L. (Solanoideae: Solaneae) and allied genera: I. a morphology-based cladistic analysis. In *Solanaceae IV, Advances in Biology and Utilization*, M. Nee, D.E. Symon, J.P. Jessop & J.G. Hawkes. (eds.) Royal Botanic Gardens, Kew, this volume.
- Felsenstein, J. 1978. Cases in which parsimony and compatibility methods will be positively misleading. *Syst. Zool.* 27: 401–410.
- Hennig, W. 1966. *Phylogenetic Systematics*. Univ. Illinois Press, Urbana, Illinois.
- Hosaka, K., Ogihara, Y., Matsubayashi, M., & Tsunewaki, K. 1984. Phylogenetic relationship between the tuberous *Solanum* species as revealed by restriction endonuclease analysis of chloroplast DNA. *Jap. J. Genet.* 59: 349–369.
- Hunziker, A.T. 1979. South American Solanaceae: a synoptic survey. In J.G. Hawkes, R.N. Lester, & A.D. Skelding (eds.), *The Biology and Taxonomy of the Solanaceae*, pp. 49–86. Academic Press, London.
- Hunziker, A.T. 1995. Studies on Solanaceae XXXVIII. Miscellaneous novelites on the taxonomy of Solanaceae. *Lorentzia* 8: 5–8.
- Johnson, L.A. & Soltis, D.E. 1995. Phylogenetic inference using *matK* sequences. *Ann. Missouri Bot. Gard.* 82: 149–175.
- Keeley, S.C. & Jansen, R.K. 1991. Evidence from chloroplast DNA for the recognition of a new tribe, the Tarchonantheae, and the tribal placement of *Pluchea* (Asteraceae). *Syst. Bot.* 16: 173–181.
- Kung, S.D., Zhu, Y.S., & Chen, K. 1982. *Nicotiana* chloroplast genome III. Chloroplast DNA evolution. *Theor. Appl. Genet.* 61: 73–79.
- Lin, C.M., Liu, Z.Q. & Kung, S.D. 1986. *Nicotiana* chloroplast genome: X. Correlation between DNA sequences and the isoelectric focusing patterns of the LS of Rubisco. *Plant Mol. Biol.* 6: 81–87.
- Linnaeus, C. 1753. *Species Plantarum*. Stockholm.

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

- Meagher, R.B., Berry-Lowe, S., & Rice, K. 1989. Molecular evolution of the small subunit of ribulose biphosphate carboxylase: nucleotide substitution and gene conversion. *Genetics* 123: 845–863.
- Miers, J. 1849. Observations upon several genera hitherto placed in Solanaceae, and upon others intermediate between the family and the Scrophulariaceae. *Ann. Mag. Nat. Hist.*, ser. 2, 3: 161–183.
- Mione, T., Olmstead, R.G., Jansen, R.K., & Anderson, G.J. 1994. Systematic implications of chloroplast DNA variation in *Jaltomata* and selected physaloid genera (Solanaceae). *Amer. J. Bot.* 81: 912–918.
- Olmstead, R.G., Jansen, R.K., Michaels, H.J., Downie, S.R., & Palmer, J.D. 1990. Chloroplast DNA and phylogenetic studies in the Asteridae. In S. Kawano (ed.), *Biological Approaches and Evolutionary Trends in Plants*, pp. 119–134. Academic Press, London.
- Olmstead, R.G. & Palmer, J. 1991. Chloroplast DNA and systematics of the Solanaceae. In J.G. Hawkes, R.N. Lester, M. Nee, & N. Estrada-R. (eds.), *Solanaceae III: Taxonomy, Chemistry, Evolution*, pp. 161–168. Royal Botanic Gardens, Kew.
- Olmstead, R.G. & Palmer, J.D. 1992. A chloroplast DNA phylogeny of the Solanaceae: subfamilial relationships and character evolution. *Ann. Missouri Bot. Gard.* 79: 346–360.
- Olmstead, R.G., Michaels, H.J., Scott, K.M., & Palmer, J.D. 1992. Monophyly of the Asteridae and identification of their major lineages inferred from DNA sequences of *rbcl*. *Ann. Missouri Bot. Gard.* 79: 249–265.
- Olmstead, R.G., Bremer, B., Scott, K., & Palmer, J.D. 1993a. A parsimony analysis of the Asteridae sensu lato based on *rbcl* sequences. *Ann. Missouri Bot. Gard.* 80: 700–722.
- Olmstead, R.G., Sweere, J.A., & Wolfe, K.H. 1993b. Ninety extra nucleotides in *ndhF* gene of tobacco chloroplast DNA; a summary of revisions to the 1986 genome sequence. *Pl. Mol. Biol.* 22: 1191–1193.
- Olmstead, R.G. & Sweere, J.A. 1994. Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the Solanaceae. *Syst. Biol.* 43: 467–481.
- Olmstead, R.G. & Palmer, J.D. 1994. Chloroplast DNA systematics: a review of methods and data analysis. *Amer. J. Bot.* 81: 1205–1224.
- Olmstead, R.G. & Palmer, J.D. 1997. *Solanum*: implications for phylogeny, classification, and biogeography from cpDNA restriction site variation. *Syst. Bot.* 22: 19–29.
- Olmstead, R.G. & Reeves, P.A. 1995. Polyphyletic origin of the Scrophulariaceae: evidence from *rbcl* and *ndhF* sequences. *Ann. Missouri Bot. Gard.* 82: 176–193.
- Palmer, J.D. 1991. Plastid chromosomes: structure and evolution. In L. Bogorad & I. K. Vasil (eds.), *The Molecular Biology of Plastids (Cell Culture and Somatic Cell Genetics of Plants, Vol. 7a)*, pp. 5–53. Academic Press, San Diego.
- Palmer, J.D. & Zamir, D. 1982. Chloroplast DNA evolution and phylogenetic relationships in *Lycopersicon*. *Proc. Nat. Acad. Sci. U.S.A.* 79: 5006–5010.
- Palmer, J.D., Jansen, R.K., Michaels, H.J., Chase, M.W., & Manhart, J.W. 1988. Chloroplast DNA variation and plant phylogeny. *Ann. Missouri Bot. Gard.* 75: 1180–1206.
- Persson, V., Knapp, S., & Blackmore, S. 1994. Pollen morphology and systematics of tribe Juanulloae A. T. Hunziker (Solanaceae). *Rev. Paleo. Palyn.* 83: 1–30.
- Persson, V., Knapp, S., & Blackmore, S. 1995. *Datura* and *Brugmansia* revisited. In *Solanaceae IV, Advances in Biology and Utilization*, M. Nee, D.E. Symon, J.P. Jessop & J.G. Hawkes, (eds.) Royal Botanic Gardens, Kew, this volume.
- Scotland, R.W., Sweere, J.S., Reeves, P.A., & Olmstead, R.G. 1995. Higher level systematics of Acanthaceae determined by chloroplast DNA sequences. *Amer. J. Bot.* 82: 266–275.

- Shinozaki, K., Ohme, M., Tanaka, M., Wakasugi, T., Hayashida, N., Matsubayashi, T., Zaita, N., Chunwongse, J., Obokata, J., Yamaguchi-Shinozaki, K., Ohto, C., Torazawa, K., Meng, B.Y., Sugita, M., Deno, H., Kamogashira, T., Yamada, K., Kusuda, J., Takaiwa, F., Kata, A., Tohdoh, N., Shimada, H., & Sugiura, M. 1986. The complete nucleotide sequence of tobacco chloroplast genome: its gene organization and expression. *EMBO J.* 5: 2043–2049.
- Soltis, P.S., Soltis, D.E., & Doyle, J.J. (eds.). 1992. *Molecular systematics of plants*. 434 pp. Chapman & Hall, New York.
- Soltis, P.S., & Soltis, D.E. 1995. Plant molecular systematics: inferences of phylogeny and evolutionary processes. *Evolutionary Biology* 28: 139–194.
- Spooner, D.M., Anderson, G.J. & Jansen, R.K. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (Solanaceae). *Amer. J. Bot.* 80: 676–688.
- Sudhakaran, S. & Ganapathi, A. 1995. Biosystematic of South Indian *Physalis*. In *Solanaceae IV, Advances in Biology and Utilization*, M. Nee, D. Symon, J.P. Jessop & J.G. Hawkes, (eds.), Royal Botanic Gardens, Kew. this volume.
- Swofford, D.L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, vers. 3.1. Illinois Natural History Survey, Champaign, Illinois.
- Sytsma, K.J. & Hahn, W.J. 1994. II. Molecular Systematics: 1991–1993. *Prog. Bot.* 55: 307–333.
- Thorne, R.T. 1992. Classification and geography of the flowering plants. *Bot. Rev.* 58: 225–348.
- Wolfe, K.H., Li, W.-H., & Sharp, P.M. 1987. Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. *Proc. Natl. Acad. Sci. U.S.A.* 84: 9054–9058.
- Zhang, Z.Y. & Lu, A.M. 1995. A comparative study on *Physalis*, *Capsicum* and *Tubocapsicum* and its systematic significance. In *Solanaceae IV, Advances in Biology and Utilization*, M. Nee, D.E. Symon, J.P. Jessop & J.G. Hawkes, (eds.) Royal Botanic Gardens, Kew, this volume.

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

Appendix 1. Synoptical, phylogenetic classification by subfamily, tribe, and subtribe. Numbers in () indicate estimated number of species (primarily based on D'Arcy 1991). ? indicates genus tentatively placed.

Cestroideae

Browallieae

- Browallia* (3) South & Central America (2), North America (1)
- Streptosolen* (1) South America

Cestreae

- Cestrum* (175) South & Central America
- Metternichia* (1) South America
- Sessea* (5) South America
- Vestia* (1) South America

Salpiglossideae

- Reyesia* (4) South America
- Salpiglossis* (2) South America

Goetzeoideae

- Coeloneurum* (1) Hispaniola
- Espadaea* (1) Cuba
- Goetzea* (2) Hispaniola, Puerto Rico
- Hemoonia* (3) Cuba

Petunioideae

- Benthamiella* (12) Patagonia
- Bouchetia* (3) South & Central America
- Brunfelsia* (45) South & Central America
- Calibrachoa* (24) South & Central America
- Combera* (2) Patagonia
- Fabiana* (21) South America
- Hunzikeria* (3) Central America
- Latua?* (1) South America
- Leptoglossis* (7) South America
- Nierembergia* (36) South America
- Pantacantha* (1) South America
- Petunia* (3) South America
- Plowmania* (1) Central America

Schizanthoideae

- Schizanthus* (12) Chile

Schwenckioideae

- Heteranthia?* (1) South America
- Melananthus* (5) South America
- Protoschwenckia* (1) South America
- Schwenckia* (22) South America

X = 12 group {class without formal rank}

Nicotianoideae

Anthocercideae

- Anthocercis* (9) Australia
- Anthotroche* (3) Australia
- Crenidium* (1) Australia
- Cyphanthera* (9) Australia
- Duboisia* (3) Australia
- Grammosolen* (2) Australia
- Symonanthus* (2) Australia

Nicotianeae

- Nicotiana* (95) South & North America, Australia, Africa

Solanoideae

Capsiceae

- Capsicum* (25) South America
- Lycianthes* (200) South America, Southeast Asia

Datureae

- Brugmansia* (5) South America
- Datura* (11) Central America
- Methysticodendron* (1) (= *Brugmansia*) South America

Hyoscyameae

- Anisodus* (4) China
- Atropa* (5) Old World
- Atropanthe* (1) China
- Hyoscyamus* (20) Old World
- Physochlaina* (11) Old World
- Przewalskia* (1) China
- Scopolia* (2) Europe (1) Japan (1)

Jaboroseae

- Jaborosa* (25) South America

Solandreae

Juanulloinae

- Dyssochroma* (2) South America
- Ectozoma* (1) South America
- Hawkesiophyton* (4) South America
- Juanulloa* (9) South America
- Markea* (9) South America
- Merinthopodium* (5) South America
- Rahowardiana* (1) Central America
- Schultesianthus* (5) South America
- Trianaea* (4) South America

Solandrinae

- Solandra* (10) South & Central America

Lycieae

- Grabowskia* (6) South America
- Lycium* (80) World-wide
- Phrodus* (1) South America

Mandragoreae

- Mandragora* (4) Old World

Nicandreae

- Exodeconus?* (6) South America
- Nicandra* (1) South America

Nolaneae

- Alona* (6) South America
- Nolana* (16) South America

Physaleae

Io chrominae

- Acnistus* (1) South America
- Dunalia* (6) South America
- Io chroma* (15) South America
- Saracha* (3) South America
- Vassobia* (4) South America

Physalinae

- Brachistus* (3) Central America
- Chamaesaracha* (10) Central America
- Leucophysalis* (9) Central & North America

Phylogeny & provisional classification of the Solanaceae based on chloroplast DNA

Margaranthus (1) Central America
Oryctes (1) Southwest USA
Quincula (1) Southwest USA
Physalis (75) New World & China (1)
Witheringia (10) South & Central America

Salpichroinae

Nectouxia (1) Central America
Salpichroa (15) South America

Withaninae

Archiphysalis (3) China, Japan
Athenaea (10) South America
Aureliana (1) South America
Cuatresia (9) South America
Deprea? (8) South America
Larnax? (= *Deprea*)
Mellissia (1) St. Helena
Physaliastrum (9) Asia
Tubocapsicum (1) China
Withania (10) Canary Is. to Nepal

Solaneae

Cyphomandra (35) (= *Solanum*) South & Central America
Discopodium (1) Africa
Jaltomata (18) South & Central America
Lycopersicon (9) (= *Solanum*) South America
Normania (2) Macaronesia
Nothoestrum? (6) Hawaii
Solanum (>1,000) World-wide
Triguera (2) Old World

Incertae sedis or Doubtful genera

Duckeodendron (1) Brazil
Parabouchetia (1) Brazil
Pauia (1) Assam
Tsoala (1) Madagascar