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MAJOR CLADES IN *SOLANUM* BASED ON *ndh*F SEQUENCE DATA

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Abstract. Analysis of sequence data from the chloroplast gene *ndh*F identifies at least 12 major well-supported clades within the genus *Solanum.* These are briefly described, given informal clade names, and compared with the groups recognized by previous *Solanum* workers. Non-molecular synapomorphies are proposed for many of the clades. Continued use of informal taxonomic designations is advocated for new infrageneric groups within *Solanum.*

Key words: *ndh*F, phylogeny, Solanaceae, *Solanum*.

Solanum L., with approximately 1400 species, is the largest and most diverse genus in the Solanaceae. *Solanum* is distinguished from most of the other genera in the tribe Solaneae by its poricidal anther dehiscence, a character present in nearly all *Solanum* species and shared only with the related genus *Lycianthes.* Although some previous authors considered *Lycianthes* to be part of *Solanum,* recent molecular studies have confirmed the distinction between the two genera (Bohs & Olmstead, 1997; Olmstead & Palmer, 1997; Olmstead et al., 1999). Morphologically, *Lycianthes* is differentiated from *Solanum* by differences in calyx structure (D'Arcy, 1986).

Although poricidal anther dehiscence is a relatively striking synapomorphy that allows *Solanum* to be recognized as a genus, its division into infrageneric subunits is less clear. Early workers attempted to divide *Solanum* into two large groups based on spininess, anther morphology, or hair type. Linnaeus, for instance, divided *Solanum* into two groups, *Spinosa* and *Inermia,* based on the presence or absence of spines (Linnaeus, 1753). Dunal, in his early treatments (Dunal, 1813, 1816), maintained this distinction as his categories *Aculeata* and *Inermia,* but in his *Solanum* treatment for DeCandolle's *Prodromus* (Dunal, 1852) he established two major infrageneric divisions ("sections") based on anther shape as well as presence or absence of spines. His group *Pachystemonum* encompassed species that lack spines and have relatively short, broad anthers with large terminal pores which often enlarge into longitudinal slits, whereas *Leptostemonum* included prickly species with relatively narrow, distally tapered anthers with small terminal pores that do not elongate with age. Bitter (1919) also recognized two major infrageneric groups, the subgenera *Eusolanum* and *Leptostemonum*, based on the same characters as Dunal (1852). Seithe (1962), in contrast, divided *Solanum* into two groups based not on spininess or anther morphology, but rather on hair type. She recognized two categories in *Solanum* at the rank of "Chorus subgenerum," distinguished by the presence of unbranched or dendritically branched hairs (Chorus subgenerum *Solanum*) versus stellate hairs (Chorus subgenerum *Stellatipilum*). Danert (1970) integrated characters of branching patterns and shoot morphology with previous systems, and, along with Gilli (1970), summarized the infrageneric groups recognized by Bitter and Seithe.

These works provided the elements of D'Arcy's (1972) classification scheme and conspectus, which is the most widely used system today.

TABLE 1.

Solanum subgenera according to D'Arcy (1972, 1991).

1. *Solanum* subg. *Archaesolanum* Marzell
    ca. 8 species, Australian region
2. *Solanum* subg. *Bassovia* (Aubl.) Bitter
    ca. 15 species, New World
3. *Solanum* subg. *Leptostemonum* (Dunal) Bitter
    ca. 250–450 species, worldwide
4. *Solanum* subg. *Lyciosolanum* Bitter
    1 species, South Africa
5. *Solanum* subg. *Minon* Raf. [subg. *Brevantherum* (Seithe) D'Arcy, in D'Arcy (1972)]
    ca. 70 species, New World
6. *Solanum* subg. *Potatoe* (G. Don) D'Arcy
    ca. 300 species, worldwide
7. *Solanum* subg. *Solanum*
    200 species, worldwide

D'Arcy's scheme recognizes seven subgenera in *Solanum* (Table 1; D'Arcy, 1972, 1991). These range in size from the monotypic subgenus *Lyciosolanum* to the subgenera *Solanum*, *Leptostemonum*, and *Potatoe*, each of which contains hundreds of species. In his 1972 paper, D'Arcy lectotypified all subgeneric names and provided a provisional conspectus of *Solanum*. In this conspectus, *Solanum* subgenera, sections, and series are listed along with their respective type species, but all the component species of each infrageneric group are not listed, nor are the characters given that circumscribe each of the groups. D'Arcy (1991) made minor modifications to this system. Whalen (1984) provided a detailed conspectus of *Solanum* subg. *Leptostemonum* (the spiny solanums). Subsequently, both Nee (1999) and Child and Lester (2001) provided infrageneric schemes for *Solanum*. Nee (1999) listed the species that belong to each of his taxonomic categories, but his system includes only New World taxa. Child and Lester (2001), like D'Arcy (1972), listed only the type species for each of their infrageneric groups. Hunziker (2001) modified D'Arcy's (1972) system and provided descriptions and commentary for each recognized section. All of these classifications relied completely on morphological data and, except for Whalen (1984), none utilized techniques of cladistic analysis.

The advent of molecular data has revolutionized the field of plant systematics and has led to new insights into phylogenetic relationships at all taxonomic levels. In the Solanaceae, Olmstead and colleagues have used restriction site and sequence data to examine phylogenetic relationships across the entire family (Olmstead & Palmer, 1992; Olmstead et al., 1999). Molecular studies above the sectional level in *Solanum* include the works of Spooner et al. (1993), Olmstead and Palmer (1997), and Bohs and Olmstead (1997, 1999, 2001). These studies provide information on major clades within *Solanum*, but none have sampled from all the subgenera recognized by morphological systematists such as Bitter, Seithe, Danert, and D'Arcy.

This paper presents results of a molecular phylogenetic study designed to identify major clades within *Solanum* using sampling from a broad spectrum of *Solanum* subgroups. Results are presented from an analysis of sequence data from the chloroplast gene *ndh*F. Sampling includes members of all seven of D'Arcy's subgenera and over 40 of the 62 sections listed in D'Arcy (1991). All the sections listed in D'Arcy's (1972) conspectus as well as many sections described after 1972 are discussed in context of the major *ndh*F clades. Major lineages are described with informal clade names and their component sectional groups are listed. Possible non-molecular synapomorphies are suggested for most of the identified clades. These characters have been taken from the general references listed above and from the personal observations of the author. Although they may provide general guidelines for the recognition of clades, this is not intended to be a substitute for thorough morphological analyses, as many of the suggested characters are variable within clades and may be found in more than one clade. A few overall recommendations are made for taxonomic rearrangements within the genus *Solanum*. Results of analyses using data from nuclear genes such as ITS and *waxy* (Bohs, in prep.) and from combined chloroplast and nuclear sequence data sets will be presented in a future publication.

MATERIALS AND METHODS

Sampling comprised 120 species of Solanaceae, including five outgroup genera from the tribe Solaneae. Outgroup taxa were chosen on the basis of previously published results of Olmstead et al. (1999) and Bohs and Olmstead (2001). *Solanum* taxa sampled included representatives of all seven of D'Arcy's subgenera and a number of sections or species groups thought to represent distinctive clades based on morphology. Collection and voucher information is given in Table 2.

DNA was extracted from fresh or silica-dried leaves or, in rare cases, from herbarium specimens, using either the modified CTAB procedure of Doyle and Doyle (1987) or a microextraction protocol that used QiaQuick columns and buffer (Qiagen, Inc.) in place of the isopropanol precipitation step in the CTAB procedure. Samples

TABLE 2.

Sources of taxa sequenced for *ndh*F. [a]DNA extracts provided by: (1) L. Bohs, University of Utah, Salt Lake City, Utah; (2) R. G. Olmstead, University of Washington, Seattle, Washington; (3) T. Mione, Central Connecticut State University, New Britain, Connecticut; (4) D. Spooner, University of Wisconsin, Madison, Wisconsin; (5) A. Bruneau, McGill University, Montreal, Canada. [b]According to D'Arcy (1972, 1991) unless noted. [c]Accession numbers given for cultivated collections. BIRM = cultivated at University of Birmingham, U.K.; NIJ = cultivated at University of Nijmegen, The Netherlands; PI = U.S.D.A. Plant Introduction number; D'Arcy collection = cultivated at MO. [d]Collector, number, and herbarium acronym (if known) of herbarium vouchers. [e]Child (1998). [f]Bohs (1990). [g]Nee (1999). [h]Symon (1981). [i]D'Arcy (1992). [j]Knapp (2000).

Taxon[a]	Subgenus[b]	Section[b]	Collection locality[c]	Voucher[d]	GenBank accession number
Capsicum baccatum L. var. *pendulum* (Willd.) Eshbaugh[2]			Bolivia	*Eshbaugh 1584* (MU)	U08916
Capsicum chacoense Hunz.[2]			Bolivia	*Eshbaugh 1586A* (MU)	AF500809
Jaltomata procumbens (Cav.) J. L. Gentry[3]			Mexico	*Davis 1189A*	U47429
Jaltomata sinuosa (Miers) Mione[1]			Bolivia	*Nee et al. 51830* (NY)	AF500835
Lycianthes heteroclita (Sendtn.) Bitter[1]			Costa Rica	*Bohs 2376* (UT)	U72756
Lycianthes rantonnei (Carrière) Bitter[2]			BIRM S.0928	*RGO S-96* (WTU)	AF500840
Physalis alkekengi L.[2]			D'Arcy collection	*D'Arcy 17707* (MO)	U08927
Solanum abutiloides (Griseb.) Bitter & Lillo[2]	*Minon*	*Brevantherum*	BIRM S.0655	*RGO S-73* (WTU)	U47415
Solanum accrescens Standl. & C. V. Morton[1]	*Leptostemonum*	*Erythrotrichum*[e]	Costa Rica	*Bohs 2556* (UT)	AF500795
Solanum adhaerens Roem. & Schult.[1]	*Leptostemonum*	*Micracantha*	Costa Rica	*Bohs 2473* (UT)	AF224061
Solanum adscendens Sendtn.[1]	*Solanum*	*Gonatotrichum*	Bolivia	*Bohs & Nee 2738* (UT)	AF500796
Solanum aethiopicum L.[2]	*Leptostemonum*	*Oliganthes*	BIRM S.0344	*RGO S-74* (WTU)	AF500797
Solanum aggregatum Jacq.[2]	*Lyciosolanum*	*Lyciosolanum*	South Africa	*RGO 99-25* (WTU)	AF500798
Solanum aligerum Schltdl.[1]	*Minon*	*Holophylla*	Bolivia	*Nee et al. 51822* (NY)	AF500799
Solanum allophyllum (Miers) Standl.[1]	None[f]	*Allophyllum*[f]	Panama	*Bohs 2339* (UT)	U47416
Solanum amygdalifolium Steud.[1]	*Potatoe*	*Jasminosolanum*	Argentina	*Nee & Bohs 50840* (NY)	AF500800
Solanum aphyodendron S. Knapp[2]	*Solanum*	*Geminata*	Colombia	*RGO S-92* (WTU)	AF500801
Solanum appendiculatum Dunal[2]	*Potatoe*	*Basarthrum*	Mexico	*Anderson 1401* (CONN)	AF224062
Solanum arboreum Dunal[1]	*Solanum*	*Geminata*	Costa Rica	*Bohs 2521* (UT)	U47417

Solanum argentinum Bitter & Lillo[1]	*Minon*	*Holophylla*	Argentina	*Bohs 2539* (UT)	U72752
Solanum aviculare G. Forst.[2]	*Archaesolanum*	*Archaesolanum*	BIRM S.0809	none	U47418
Solanum betaceum Cav.[1]	Genus *Cyphomandra*	*Pachyphylla*	Bolivia	*Bohs 2468* (UT)	U47428
Solanum brevicaule Bitter[4]	*Potatoe*	*Petota*	Bolivia PI 498115	*Hawkes et al. 6701*	AF500803
Solanum bulbocastanum Dunal[4]	*Potatoe*	*Petota*	Mexico PI 347757	*Tarn 153*	AF500804
Solanum caesium Griseb.[1]	*Solanum*	*Solanum*	Bolivia	*Bohs et al. 2815* (UT)	AF500805
Solanum calileguae Cabrera[1]	*Solanum*[g]	*Dulcamara*[g]	Argentina	*Nee & Bohs 50809* (NY)	AF500806
Solanum campanulatum R. Br.[2]	*Leptostemonum*	*Campanulata*	BIRM S.0387	*RGO S-78* (WTU)	AF500807
Solanum campechiense L.[1]	*Leptostemonum*	Unclear	Costa Rica	*Bohs 2536* (UT)	AF224071
Solanum candidum Lindl.[2]	*Leptostemonum*	*Lasiocarpa*	BIRM S.0975	*RGO S-100* (WTU)	AF224072
Solanum capsicoides All.[1]	*Leptostemonum*	*Acanthophora*	Peru	*Bohs 2451* (UT)	AF500808
Solanum carolinense L.[2]	*Leptostemonum*	*Lathyrocarpum*	BIRM S.1816	*RGO S-77* (WTU)	AF500811
Solanum chenopodinum F. Muell.[2]	*Leptostemonum*	*Graciliflora*	BIRM S.0813	none	AF500812
Solanum cinereum R. Br.[1]	*Leptostemonum*	*Melongena*[h]	NIJ 904750120	*Bohs 2852* (UT)	AF500813
Solanum citrullifolium A. Braun[2]	*Leptostemonum*	*Androceras*	BIRM S.0127	*RGO S-79* (WTU)	AF500814
Solanum cleistogamum Symon[2]	*Leptostemonum*	*Oliganthes*	BIRM S.0844	*RGO S-80* (WTU)	AF500815
Solanum conditum C. V. Morton[1]	*Leptostemonum*	Unclear	Bolivia	*Bohs & Nee 2733* (NY)	AF500816
Solanum cordovense Sessé & Moç.[1]	*Minon*	*Extensum*	Costa Rica	*Bohs 2693* (UT)	U72751
Solanum crinitipes Dunal[2]	*Leptostemonum*	*Torva*	Colombia	*RGO S-81* (WTU)	AF500817
Solanum crinitum Lam.[1]	*Leptostemonum*	*Crinitum*[e]	NIJ 924750049	*Bohs 2850* (UT)	AF500818
Solanum crispum Ruiz & Pav.[2]	*Minon*	*Holophylla*	BIRM S.0486	none	AF500819
Solanum deflexum Greenm.[1]	*Solanum*	*Gonatotrichum*	Costa Rica	*Bohs 2715* (UT)	AF500820
Solanum delitescens C. V. Morton[1]	*Minon*	*Holophylla*	Argentina	*Nee & Bohs 50810* (NY)	AF500821
Solanum diploconos (Mart.) Bohs[1]	Genus *Cyphomandra*	*Pachyphylla*	Brazil	*Bohs 2335* (UT)	AY049014
Solanum doddsii Correll[4]	*Potatoe*	*Petota*	Bolivia	*Spooner et al. 6651*	AF500822
Solanum drymophilum O. E. Schulz[1]	*Leptostemonum*	*Persicariae*	Puerto Rico	*Bohs 2461* (UT)	AF500823
Solanum dulcamara L.[2]	*Potatoe*	*Dulcamara*	U.S.A.	none	U47419
Solanum echinatum R. Br.[1]	*Leptostemonum*	*Leprophora*	NIJ 954750052	*Bohs 2727* (UT)	AF500824
Solanum elaeagnifolium Cav.[2]	*Leptostemonum*	*Leprophora*	U.S.A.	*RGO S-82* (WTU)	AF224067
Solanum etuberosum Lindl.[4]	*Potatoe*	*Petota*	Chile PI 498311	*UAC 1322*	AF500825

TABLE 2 CONTINUED.

Taxon[a]	Subgenus[b]	Section[b]	Collection locality[c]	Voucher[d]	GenBank accession number
Solanum evolvulifolium Greenm.[1]	*Bassovia*	*Herpystichum*[g]	Panama	*Knapp & Mallet 9178* (BM)	AF500826
Solanum ferocissimum Lindl.[2]	*Leptostemonum*	*Graciliflora*	BIRM S.0819	*RGO S-83* (WTU)	AF500827
Solanum fiebrigii Bitter[1]	*Solanum*	*Solanum*	Bolivia	*Bohs et al. 2784* (UT)	AF500828
Solanum fraxinifolium Dunal[1]	*Potatoe*	*Basarthrum*	Costa Rica	*Bohs 2558* (UT)	AF500810
Solanum furfuraceum R. Br.[2]	*Leptostemonum*	Unclear	BIRM S.1442	*RGO S-84* (WTU)	AF500829
Solanum glaucophyllum Desf.[2]	*Solanum*	*Glaucophyllum*	D'Arcy collection	none	U72753
Solanum havanense Jacq.[1]	*Solanum*	*Diamonon*[e]	NIJ 904750122	*Bohs 3076* (UT)	AF500830
Solanum herculeum Bohs[2]	genus *Triguera*		Morocco	*Jury 13742* (RNG)	AF224065
Solanum hindsianum Benth.[1]	*Leptostemonum*	Unclear	Mexico	*Bohs 2975* (UT)	AF500831
Solanum hoehnei C. V. Morton[1]	*Leptostemonum*	*Nemorense*	Brazil	*Folli 1668* (MO)	AF500832
Solanum inelegans Rusby[1]	*Minon*	*Holophylla*	Bolivia	*Nee et al. 51813* (NY)	AF500833
Solanum ipomoeoides Chodat & Hassl.[1]	*Solanum*[g]	*Dulcamara*[g]	Bolivia	*Bohs & Nee 2766* (UT)	AF500834
Solanum jamaicense Mill.[2]	*Leptostemonum*	*Eriophylla*	BIRM S.1209	*RGO S-85* (WTU)	AF224073
Solanum jasminoides Paxton[2]	*Potatoe*	*Jasminosolanum*	Colombia	*RGO S-86* (WTU)	AF500836
Solanum juglandifolium Dunal[4]	*Potatoe*	*Petota*	Colombia	LA 2788	AF500837
Solanum laciniatum Aiton[1]	*Archaesolanum*	*Archaesolanum*	New Zealand	*Bohs 2528* (UT)	U47420
Solanum lepidotum Dunal[1]	*Minon*	*Lepidotum*	Costa Rica	*Bohs 2621* (UT)	AF500838
Solanum lidii Sunding[1]	*Leptostemonum*	*Nycterium*	NIJ 934750022	*Bohs 2903* (UT)	AF500839
Solanum luteoalbum Pers.[1]	Genus *Cyphomandra*	*Cyphomandropsis*	BIRM S.0042	*Bohs 2337* (UT)	U72749
Solanum lycopersicum L.[2]	Genus *Lycopersicon*	*Lycopersicon*	U.S.A. (cult.)	none	U08921
Solanum macrocarpon L.[2]	*Leptostemonum*	*Melongena*	BIRM S.0133	*RGO S-88* (WTU)	AF224068
Solanum mahoriense D'Arcy & Rakot.[1]	*Leptostemonum*	*Cryptocarpum*[i]	Madagascar	*Bohs 2576* (UT)	AF500841
Solanum mammosum L.[2]	*Leptostemonum*	*Acanthophora*	BIRM S.0983	*RGO S-89* (WTU)	AF224074
Solanum mapiriense Bitter[1]	None[f]	*Allophyllum*[f]	Bolivia	*Nee & Solomon 30305* (UT)	AF500842
Solanum mauritianum Scop.[2]	*Minon*	*Brevantherum*	BIRM S.0860	*RGO S-90* (WTU)	AF500843

Solanum melongena L.[2]	*Leptostemonum*	*Melongena*	BIRM S.0657	*RGO S-91* (WTU)	AF224069
Solanum montanum L.[1]	*Potatoe*	*Regmandra*	NIJ 904750205	*Bohs 2870* (UT)	AF500844
Solanum multifidum Ruiz & Pav.[1]	*Potatoe*	*Regmandra*	NIJ 904750205	*Bohs 2863* (UT)	AF500845
Solanum muricatum Aiton[2]	*Potatoe*	*Basarthrum*	Colombia	*RGO S-93* (WTU)	AF500846
Solanum nemorense Dunal[1]	*Leptostemonum*	*Nemorense*	Bolivia	*Bohs & Nee 2757* (UT)	AF500847
Solanum nitidum Ruiz & Pav.[1]	*Minon*	*Holophylla*	Bolivia	*Nee 31944* (NY)	AF224075
Solanum ochrophyllum Van Heurck & Müll. Arg.[1]	*Solanum*	*Geminata*	Bolivia	*Bohs & Nee 2805* (UT)	AF500848
Solanum palitans C. V. Morton[1]	*Solanum*	*Parasolanum*	BIRM S.0837/70	*Bohs 2449* (UT)	AF224064
Solanum phaseoloides Pol.[1]	*Bassovia*	*Herpystichum*	Costa Rica	*Bohs 2485* (UT)	AF500849
Solanum physalifolium Rusby var. *nitidibaccatum* (Bitter) Edmonds[1]	*Solanum*	*Solanum*	U.S.A.	*Bohs 2467* (UT)	U47421
Solanum pinnatisectum Dunal[4]	*Potatoe*	*Petota*	Mexico PI 347766	*Tarn 205A*	AF500850
Solanum piurae Bitter[4]	*Potatoe*	*Petota*	Peru PI 310997	*Hawkes 2443*	AF500851
Solanum prinophyllum Dunal[1]	*Leptostemonum*	*Oliganthes*[h]	NIJ 904750171	*Bohs 2725* (UT)	AF500852
Solanum pseudocapsicum L.[2]	*Minon*	*Pseudocapsicum*	BIRM S.0870	none	U47422
Solanum ptychanthum Dunal[2]	*Solanum*	*Solanum*	U.S.A.	*RGO S-94* (WTU)	U47423
Solanum pubigerum Dunal[1]	*Minon*	*Holophylla*	NIJ 904750104	none	AF500853
Solanum pyracanthum Lam.[2]	*Leptostemonum*	*Oliganthes*	cult. (UCSB Bot. Gard.)	*RGO S-95* (WTU)	AF500854
Solanum quadrangulare L.f.[2]	*Solanum*	*Quadrangulare*	South Africa	*RGO 99-46* (WTU)	AF500855
Solanum riojense Bitter[1]	*Solanum*	*Episarcophyllum*	Argentina	*Nee & Bohs 50843* (NY)	AF500856
Solanum rostratum Dunal[1]	*Leptostemonum*	*Androceras*	U.S.A.	none	U47424
Solanum rovirosanum Donn. Sm.[1]	*Solanum*	*Geminata*	Costa Rica	*Bohs 2919* (UT)	AF500857
Solanum rugosum Dunal[1]	*Minon*	*Brevantherum*	Costa Rica	*Bohs 3011* (UT)	AF500858
Solanum sandwicense Hook. & Arn.[1]	*Leptostemonum*	*Irenosolanum*	Hawaii	*Bohs 2992* (UT)	AF500859
Solanum schimperianum Hochst.[2]	*Leptostemonum*	*Torva*	BIRM S.1538	*RGO S-97* (WTU)	AF500860
Solanum schlechtendalianum Walp.[1]	*Minon*	*Extensum*	Costa Rica	*Bohs 2915* (UT)	AF500861
Solanum seaforthianum Andrews[2]	*Potatoe*	*Jasminosolanum*	BIRM S.0051	none	U47425
Solanum sisymbriifolium Lam.[1]	*Leptostemonum*	*Cryptocarpum*	Argentina	*Bohs 2533* (UT)	AF500862
Solanum stenophyllidium Bitter[1]	*Potatoe*	*Petota*	NIJ 904750079	*Bohs 2855* (UT)	AF500802
Solanum stramonifolium Jacq.[5]	*Leptostemonum*	*Lasiocarpa*	Peru	*Whalen 860* (HUT)	AF500863

TABLE 2 CONTINUED.

Taxon[a]	Subgenus[b]	Section[b]	Collection locality[c]	Voucher[d]	GenBank accession number
Solanum terminale Forssk.[1]	*Solanum*	*Afrosolanum*	NIJ 814750072	*Bohs 2719* (UT)	AF500864
Solanum thelopodium Sendtn.[1]	Unclear[j]	Unclear[j]	Bolivia	*Nee & Bohs 50858* (NY)	AF500865
Solanum toliaraea D'Arcy & Rakot.[1]	*Leptostemonum*	Unclear[i]	Madagascar	*Bohs 2574* (UT)	AF500866
Solanum torvum Sw.[2]	*Leptostemonum*	*Torva*	BIRM S.0839	*RGO S-101* (WTU)	L76286
Solanum tridynamum Dunal[2]	*Leptostemonum*	*Nycterium*	BIRM S.1831	*RGO S-102* (WTU)	AF500867
Solanum triflorum Nutt.[1]	*Solanum*	*Parasolanum*	U.S.A.	*Bohs 3062* (UT)	AF500868
Solanum tripartitum Dunal[1]	*Solanum*	*Parasolanum*	BIRM S.0708/71	*Bohs 2465* (UT)	U72750
Solanum trisectum Dunal[1]	*Potatoe*	*Normania*	France	*Bohs 2718* (UT)	AF224063
Solanum trizygum Bitter[1]	*Bassovia*	*Pteroidea*	Costa Rica	*Bohs 2511* (UT)	U72754
Solanum tuberosum L.[2]	*Potatoe*	*Petota*	U.S.A. (cult.) PI (245793 X 245796)	WRF 1610 USDA NRSP-6	L76287
Solanum turneroides Chodat[1]	*Solanum*	*Gonatotrichum*	Bolivia	*Nee et al. 51716* (NY)	AF500869
Solanum uleanum Bitter[1]	*Bassovia*	*Pteroidea*	D'Arcy collection	*Bohs 2720* (UT)	AF500870
Solanum vespertilio Aiton[2]	*Leptostemonum*	*Nycterium*	BIRM S.2091	*RGO S-103* (WTU)	AF224070
Solanum villosum Mill.[1]	*Solanum*	*Solanum*	Iran PI 304600	*Bohs 2553* (UT)	AF224066
Solanum wallacei (A. Gray) Parish[1]	*Potatoe*[e]	*Californisolanum*[e]	U.S.A.	*Bohs 2438* (UT)	U47426
Solanum wendlandii Hook. f.[2]	*Leptostemonum*	*Aculeigerum*	BIRM S.0488	none	U47427
Witheringia solanacea L'Hér.[1]			Costa Rica	*Bohs 2416* (UT)	U72755

extracted with the modified CTAB method were purified using cesium chloride density gradient centrifugation or a phenol-chloroform protocol. Amplification and sequencing of the *ndh*F gene used the primers and PCR program given in Bohs and Olmstead (1997). PCR products were cleaned using QiaQuick spin columns and sequenced on an ABI automated sequencer. Sequences were edited and contigs assembled using the program Sequencher (Gene Codes Corp.). After a consensus sequence was obtained, it was aligned by eye to a template sequence (*Nicotiana tabacum* L.). Base changes relative to the template sequence were then double-checked against the chromatograms. No alignment difficulties were encountered in assembling the sequences into a data set in NEXUS file format. All new sequences reported here have been submitted to GenBank (Table 2). The data set and resultant phylogenetic trees have been submitted to TreeBASE (accession numbers S735 and M1167).

The data matrix was analyzed using unweighted parsimony with the program PAUP*4.0b10 (Swofford, 2002). The analysis used the heuristic search algorithm with the TBR and MulTrees options, 714 random addition replicates with rearrangements limited to 100,000 per replicate, and gaps treated as missing data. Trees were rooted using *Physalis alkekengi* as the outgroup. Bootstrap analyses were performed with 500 replicates using the heuristic search option, TBR and MulTrees, MaxTrees set to 1000, and 1,000,000 rearrangements per replicate.

The data were also analyzed using the parsimony ratchet (Nixon, 1999) as implemented in the program PAUPRat (Sikes & Lewis, 2001). Five replicate searches of 200 iterations each were performed. The shortest trees from all searches were retained and combined into a single consensus tree.

The same data matrix was analyzed by maximum likelihood using the program fastDNAml (Olsen et al., 1994) on a UNIX platform computer. Parameters used in the analysis were a transition/transversion ratio of 1.0006 (estimated using ML in PAUP from a neighbor-joining tree of the 120-taxon data set), empirical base frequencies (A = 0.27665, C = 0.15518, G = 0.18366, T = 0.38450), and random addition order.

RESULTS

The *ndh*F sequences obtained for all taxa except *Lycianthes heteroclita*, *Solanum wendlandii*, *S. diploconos*, and *S. deflexum* were 2086 base pairs long, corresponding to positions 24 through 2109 in the tobacco *ndh*F sequence. *Lycianthes heteroclita* had a 15 bp insertion, *S. wendlandii* had a 33 bp insertion, and *S. diploconos* had a 24 bp insertion between positions 1476 and 1477. *Solanum deflexum* had a 9 bp deletion between positions 1703 and 1711.

Of 2119 total characters in the data set, 541 were variable and 288 of these were parsimony-informative. Pairwise sequence divergence calculated using the Kimura 2-parameter model ranged from 3.4% between *S. candidum* versus *Lycianthes heteroclita* to 0.048% in the closely related species pairs *S. ferocissimum* versus *S. chenopodinum*, *S. vespertilio* versus *S. liddii*, *S. doddsii* versus *S. stenophyllidium*, and *S. piurae* versus *S. doddsii*. *Solanum schlechtendalianum* and *S. lepidotum* had identical *ndh*F sequences.

The available memory capacity of PAUP on a Power Macintosh G4 was reached after saving 18,200 most parsimonious trees from 714 random addition replicates. These trees were 1053 steps long with a CI (excluding uninformative characters) of 0.497 and RI of 0.819. PAUPRat saved 992 trees of 1053 steps out of 1000 iterations. The strict consensus trees from the heuristic parsimony and the PAUPRat searches were nearly identical, differing only in greater resolution at two of the branch tips in the PAUPRat consensus tree (not shown). Likewise, the maximum likelihood topology (not shown) was virtually identical to the parsimony trees and included the same taxa in the major clades described below. This analysis was completed overnight, examined 39,626 trees, and resulted in a tree with a log likelihood of –13487.40739.

In these trees, *Solanum* forms a monophyletic clade, with members of the former genera *Lycopersion*, *Cyphomandra*, *Normania*, and *Triguera* nested within it (Fig. 1). Species of all these genera have been transferred to *Solanum* (Spooner et al., 1993; Bohs, 1995; Bohs & Olmstead, 2001). *Capsicum* plus *Lycianthes* emerges as the sister group to the *Solanum* clade with bootstrap support of 70%. *Solanum* plus the genera *Jaltomata*, *Lycianthes*, and *Capsicum* form a well-supported clade (bootstrap = 100%), and *Lycianthes* plus *Capsicum* form a well-supported group (bootstrap = 89%).

At least 12 major clades can be discerned within *Solanum* (Fig. 1, see pp. 48–49). These clades are supported with bootstrap values ranging from 51% (Leptostemonum s.l.) to 100% (the Regmandra, Archaesolanum, and Normania clades). However, the relationships among these major clades are unclear, because for the most part they form a polytomy at the base of *Solanum*. Several of these clades conform to infrageneric groups recognized by previous systematists, but others do not.

These clades have been given informal clade names and are briefly described below with a list of their constituent sections and non-molecular synapomorphies that may define them. Asterisks (*) indicate sections or species groups that have been sampled in the present analysis. Other groups listed under each clade are inferred to belong there due to morphological similarity. Brief comparisons are made with reference to D'Arcy's (1972) classification and with several other schemes.

DISCUSSION

Major clades defined by *ndh*F data:

1. Thelopodium clade

3 spp., South America

Included taxa:

Solanum thelopodium species group *sensu* Knapp (2000)*

This group is morphologically distinctive due to its enlarged roots, single-stemmed growth habit, reduced number of sympodia, and narrow, tapered, dimorphic anthers. It was revised recently by Knapp (2000), who recognized three species. One of them, *S. thelopodium*, was included in the *ndh*F analysis, where it forms a single branch at the very base of *Solanum*. This placement is surprising and has not been suggested by recent Solanaceae systematists, although Bitter thought that *S. thelopodium* was sufficiently distinct to merit generic rank (Knapp, 2000). Dunal (1852) and Seithe (1962) placed *S. thelopodium* into *Solanum* sect. *Anthoresis* (Dunal) Bitter, but this means little, as section *Anthoresis* is a catch-all group of disparate taxa. D'Arcy did not include it in either of his summary classifications (D'Arcy, 1972, 1991). Nee (1999) put this species into *Solanum* sect. *Pteroidea* (Potato clade), but the *ndh*F data do not support this placement. Further sampling is needed to determine if the basal position of this clade in *Solanum* is correct or is perhaps a long branch artifact.

2. Regmandra clade

ca. 7 spp., South America

Included taxa:

Solanum subg. *Potatoe* (G. Don) D'Arcy pro parte

Solanum sect. *Regmandra* (Dunal) D'Arcy*

D'Arcy (1972, 1991) placed this small group of species from Pacific coastal deserts of South America into *Solanum* subg. *Potatoe*. Nee (1999) also allied this section with the potatoes, whereas Child and Lester (2001) put it into *Solanum* subg. *Solanum*, and Hunziker (2001) considered its subgeneric position uncertain. Taxa of *Solanum* sect. *Regmandra* included in the *ndh*F data set are *S. montanum* and *S. multifidum*, and they fall out together on a well-supported but isolated clade near the base of *Solanum*.

Non-molecular characters that may distinguish this clade include herbaceous habit and usually pinnately dissected and rather thick leaves, sometimes with winged petioles and stems. Plants of *Solanum montanum* and *S. multifidum* grown in the University of Utah greenhouse had nearly rotate corollas and notably expanded stigmas. *Solanum montanum* is reported to bear tubers (Dunal, 1852; Macbride, 1962), but the *ndh*F results do not suggest a direct relationship between the Regmandra clade and the tuber-bearing members of the Potato clade.

3. Archaesolanum clade

ca. 8 spp., Australia, New Guinea,
New Zealand

Included taxa:

Solanum subg. *Archaesolanum* Marzell

Solanum sect. *Archaesolanum*
(Marzell) Danert*

This is a distinctive group with no obvious close relatives within *Solanum*. It is distinguished by its aneuploid chromosome number based on $n = 23$, a number unique in the genus. All species of this group occur in Australia and the South Pacific (New Guinea, Australia, Tasmania, New Zealand). Aside from its chromosome number, possible non-molecular synapomorphies of this clade include plurifoliate sympodial units, rotate corollas with abundant interpetalar tissue, loosely erect anthers on relatively long filaments, and fruits with abundant stone cell aggregates. The basal position of this clade may indicate a relatively old radiation in the South Pacific.

The Archaesolanum clade has been recognized as distinct by virtually all previous *Solanum* workers, including D'Arcy (1972, 1991), Bitter in Marzell (1927), Danert (1970), and Symon (1994). Olmstead and Palmer (1997) included *S. aviculare* in their analysis of *Solanum* using chloroplast restriction site data, and it formed a clade with 76% bootstrap support along with *S. ptychanthum*, *S. crispum*, *S. dulcamara*, and *S. jasminoides*. However, sampling within non-spiny *Solanum* taxa was sparse in their study, with 17 non-spiny representatives out of 36 total *Solanum* species. Bohs and Olmstead (2001) found that *S. aviculare* and *S. laciniatum* formed a well-supported basal clade in *Solanum* in analyses using nuclear ITS sequence data as well as ITS combined with *ndh*F data. It seems safe to say that the Archaesolanum clade represents an isolated group whose closest relatives have not yet been identified.

4. Normania clade

3 spp., Macaronesia, Spain, NW Africa

Included taxa:

Solanum sect. *Normania* (Lowe) Bitter
[genus *Normania* Lowe]*
genus *Triguera* Cav.*

This clade includes two enigmatic groups endemic to Macaronesia and adjacent areas of Spain and northwestern Africa. Although these taxa have been recognized as the segregate genera *Normania* and *Triguera*, molecular data indicate that both are nested within *Solanum* and the three species of both genera have been transferred to *Solanum* (Bohs & Olmstead, 2001). Francisco-Ortega et al. (1993) made a thorough morphological analysis of *Normania* and *Triguera* and concluded that they were closely related.

Numerous non-molecular characters unite the species of the Normania clade, including herbaceous or weakly woody habit, foliaceous and accrescent calyces, zygomorphic corollas, subequal to very unequal stamens, anther dehiscence by both apical pores and longitudinal slits, anthers with horned projections, fruits dry or with sparse pulp, seeds large and few per fruit with the seed coat cell walls radially expanded, and pollen grains with colpi joined at the poles. Affinities of the Normania clade within *Solanum* are presently obscure. In combined analyses of *ndh*F and ITS data this clade forms a group with members of the Potato and Morelloid/Dulcamaroid clade (Bohs & Olmstead, 2001), but this placement is poorly supported, with a bootstrap value of 17%. As with the Archaesolanum clade, the Normania clade appears to form an isolated group within *Solanum* without obvious close relatives.

5. African non-spiny clade

ca. 7 spp., Africa

Included taxa:

- *Solanum* subg. *Lyciosolanum* Bitter*
- *Solanum* subg. *Solanum* pro parte
    - *Solanum* sect. *Afrosolanum* Bitter*
    - *Solanum* sect. *Quadrangulare* Bitter*
    - *Solanum* sect. *Benderianum* Bitter

D'Arcy (1972, 1991) recognized *Solanum* subg. *Lyciosolanum* as monotypic, with *S. aggregatum* as its sole member, but the *ndh*F data indicate that probably this group should be expanded to include members of *Solanum* sects. *Afrosolanum*, *Quadrangulare*, and perhaps *Benderianum*, all placed by D'Arcy (1972, 1991) in *Solanum* subg. *Solanum*. This clade forms an isolated group within *Solanum*. It is poorly known taxonomically, but possible non-molecular synapomorphies may include shrubby or climbing habit, unbranched or dendritically branched hairs, and purple or white stellate corollas. This group needs better molecular sampling and morphological characterization.

No DNA samples are available from representatives of *Solanum* sects. *Lemurisolanum* Bitter and *Macronesiotes* Bitter, two non-spiny sections endemic to Madagascar. Their affinities may lie with the African non-spiny clade or with the Dulcamaroid clade.

6. Potato clade

ca. 200–300 spp., New World

Included taxa:

- *Solanum* subg. *Potatoe* (G. Don) D'Arcy pro parte
    - *Solanum* sect. *Petota* Dumort.*
    - *Solanum* sect. *Anarrhichomenum* Bitter*
    - *Solanum* sect. *Basarthrum* (Bitter) Bitter*
    - *Solanum* sect. *Lycopersicon* (Mill.) Wettst.*
    - *Solanum* sect. *Neolycopersicon* Correll
    - *Solanum* sect. *Juglandifolium* (Rydb.) A. Child*
    - *Solanum* sect. *Etuberosum* (Bukasov & Kamaraz) A. Child*
    - *Solanum* sect. *Articulatum* (Correll) A. Child
    - *Solanum* sect. *Taeniotrichum* A. Child
- *Solanum* subg. *Bassovia* (Aubl.) Bitter pro parte
    - *Solanum* sect. *Herpystichum* Bitter*
    - *Solanum* sect. *Pteroidea* Dunal*

This clade includes most of the groups of D'Arcy's subgenera *Potatoe* and *Bassovia*. Child's treatment of subgenus *Potatoe* (Child, 1990; Child & Lester, 2001) included these groups, but his concept also encompassed a number of disparate elements that are placed here in different clades, such as *Solanum* sect. *Normania* (here placed in the Normania clade), the dulcamaroid taxa *sensu* Child and Lester (2001; sects. *Dulcamara*, *Jasminosolanum*, and *Californisolanum*, here placed in the Dulcamaroid clade), and the "anomalously prickly" taxa *sensu* Child (1990; sects. *Aculeigerum*, *Nemorense*, and *Herposolanum*, here placed in the Wendlandii/Allophyllum and Leptostemonum clades). Nee's recent *Solanum* scheme (Nee, 1999) considered the taxa that here belong to the Potato clade to represent two distinct evolutionary lines. He included the potatoes and their relatives (sects. *Petota*, *Anarrhichomenum*, *Basarthrum*) in a large and morphologically diverse subgenus *Solanum*, along with other groups such as sections *Dulcamara*, *Solanum*, *Holophylla*, *Brevantherum*, *Regmandra*, and *Archaesolanum*. He also included members of section *Herpystichum* in this clade. As Nee (1999) noted, the type of section *Herpystichum* is not known with certainty and the group is not well circumscribed, but he listed *S. phaseoloides* and *S. evolvulifolium* as members of the section. These species are sampled in the *ndh*F analyses, and they both fall out in the Potato clade.

On the other hand, Nee (1999) maintained *Solanum* subg. *Bassovia*, amplifying it to include sections *Cyphomandropsis* and *Pachyphylla* of the Cyphomandra clade and section *Allophylla* of the Wendlandii/Allophyllum clade along with section *Pteroidea*, which was placed in subgenus *Bassovia* by previous workers such as Bitter (1921), Seithe (1962), Danert (1970), and D'Arcy (1972). Knapp and Helgason (1997) revised the species of section *Pteroidea*, but they were unsure of the higher-level relationships of the section.

The *ndh*F data indicate that section *Pteroidea* belongs to the Potato clade, and that the sampled representatives of the subgenera *Potatoe* and *Bassovia sensu* D'Arcy (1972) each form monophyletic clades. Non-molecular synapomorphies that may unite both of these groups include herbaceous to weakly woody and often scandent habit, exclusively unbranched hairs, presence of rhizomes or tubers in many taxa, presence of compound leaves in most species, and lack of stone cell aggregates in the fruits. The presence of solanidine/tomatidine alkaloids may be the most consistent synapomorphy that defines the subgenus *Potatoe*. Whether members of the subgenus *Bassovia* possess these types of alkaloids is unknown.

Child (1990) placed *Solanum evolvulifolium* in section *Anarrhichomenum*, whereas Nee (1999) placed this species in section *Herpystichum*. The *ndh*F data show that *S. evolvulifolium* is more closely related to *S. phaseoloides* (sect. *Herpystichum*) than to *S. appendiculatum* (sect. *Anarrhichomenum*).

The placement of this monotypic *Solanum* sect. *Rhynchantherum* Bitter has been debated. Dunal (1852), D'Arcy (1972, 1991), and Hunziker (2001) assigned it to subgenus *Potatoe*, Bitter (1913a) proposed an affinity with *S. reptans* of section *Herposolanum* (cf. *S. hoehnei* in the Leptostemonum clade), and Miers (1855) and Child (1984b; Child & Lester, 2001) placed it in the genus *Cyphomandra* (Cyphomandra clade). Although no DNA data are available, its pinnately compound leaves and anther structure (described in Bohs, 1994) argue for placement in the Potato clade.

7. Morelloid/Dulcamaroid clade

This group comprises two subclades, which will be discussed separately. Bootstrap support for the association of the two groups is strong (94% of bootstrap replicates) in the *ndh*F data set, but additional molecular data from other genes are needed to ascertain whether this group should be better recognized as two separate clades. For instance, ITS data from a small subset of the taxa considered here provided weak support (19% of bootstrap replicates) for the association of the morelloid and dulcamaroid subgroups (Bohs & Olmstead, 2001).

7a. Morelloid clade

ca. 75 spp., worldwide

Included taxa:

- *Solanum* subg. *Solanum* pro parte
  - *Solanum* sect. *Solanum**
  - *Solanum* sect. *Campanulisolanum* Bitter*
  - *Solanum* sect. *Parasolanum* A. Child*
  - *Solanum* sect. *Episarcophyllum* Bitter*
  - *Solanum* sect. *Chamaesarachidium* Bitter

This clade includes the core of *Solanum* species often known as the morelloid taxa. The four sections exclusive of section *Parasolanum* are morphologically homogeneous, and sectional distinctions are not clear-cut. Three members of *Solanum* sect. *Parasolanum* (*S. tripartitum*, *S. palitans, S. triflorum*) were sampled in the *ndh*F analyses, and all are included in the morelloid clade. However, these three taxa do not fall out together, indicating that section *Parasolanum* as circumscribed by Child (1984a) may not be a monophyletic group. In the *ndh*F analyses, *S. tripartitum* and *S. palitans* form a strongly supported clade, which, in turn, is strongly associated with the rest of the Morelloid clade (95% bootstrap support). However, these two species form a separate group distinct from the rest of the Morelloid clade in trees based on ITS sequences (Bohs & Olmstead, 2001). More extensive ITS sampling along with molecular data from additional genes may enhance the circumscription and placement of section *Parasolanum*.

Some non-molecular characters that may serve to unite this clade include herbaceous or weakly woody habit, 2- to 3-foliate sympodial units, pubescent filaments and styles in many taxa, and small stone cell aggregates in the fruits.

7b. Dulcamaroid clade

ca. 40 spp., worldwide

Included taxa:

Solanum subg. *Potatoe* (G. Don) D'Arcy pro parte

- *Solanum* sect. *Dulcamara* Dumort.*
- *Solanum* sect. *Jasminosolanum* Seithe*
- *Solanum* sect. *Californisolanum* A. Child*

Solanum subg. *Solanum* pro parte

- *Solanum* sect. *Lysiphellos* (Bitter) Seithe

Solanum subg. *Minon* Raf. pro parte

- *Solanum* sect. *Holophylla* Walp. pro parte*

This clade consists of elements from three of D'Arcy's subgenera. Sectional limits are not well defined, and the majority of groups included here are in need of critical taxonomic revision and nomenclatural clarification. The *ndh*F results indicate that *Solanum* sect. *Holophylla* is not monophyletic as traditionally defined. Part of *Solanum* sect. *Holophylla* that includes the species *S. aligerum*, *S. pubigerum*, and members of the *S. nitidum* group [Knapp, 1989; equivalent to *S.* subsect. *Nitidum* A. Child (Child, 1998)] belongs to the Dulcamaroid clade. At least part of the remainder of *Solanum* sect. *Holophylla*, represented in the *ndh*F trees by *S. argentinum*, belongs to the Geminata clade. Morphological synapomorphies of the Dulcamaroid clade may include vining habit in many taxa, the presence of unbranched, dendritic, or echinoid hairs, 3- to many-foliate sympodial units, and fruits lacking stone cell aggregates.

The following clades form a large group in *Solanum* with 98% bootstrap support (Fig. 1). Although the majority of species in this group belong to the spiny *Solanum* subg. *Leptostemonum* (the Leptostemonum clade), four other predominantly non-spiny clades are represented here. This group is morphologically heterogeneous and has not been recognized formally at any rank.

8. Wendlandii/Allophyllum clade

ca. 10 spp., New World

Included taxa:

- *Solanum* sect. *Allophyllum* (Child) Bohs*

Solanum subg. *Leptostemonum* pro parte

- *Solanum* sect. *Aculeigerum* Seithe*

This clade is perhaps the most unusual and surprising in all of *Solanum*. Thus far it consists of two groups whose relationships to other *Solanum* taxa have been debated. Species of *Solanum* sect. *Allophyllum* were previously placed in the genus *Cyphomandra* (D'Arcy, 1973; Child, 1984b; Bohs, 1988), but Bohs (1989) showed that they did not have the characters of the Cyphomandra clade. The subgeneric placement of *Solanum* sect. *Allophyllum*, however, has been obscure (Bohs, 1990). *Solanum* sect. *Aculeigerum* has usually been placed in subgenus *Leptostemonum* because the plants bear spines (D'Arcy, 1972, 1991; Whalen, 1984). However, they lack stellate hairs, a hallmark of the subgenus, so some workers have placed this section in with the non-spiny species of *Solanum* in either subgenus *Solanum* (Seithe, 1962) or *Potatoe* (Child, 1990; Child & Lester, 2001). Molecular data of Bohs and Olmstead (1997, 1999, 2001) showed that *Solanum* sect. *Aculeigerum* probably does not belong in the spiny *Solanum* subg. *Leptostemonum*, but is instead allied to a spineless group, section *Allophyllum*. The *ndh*F analyses presented here continue to support that placement. Species of *Solanum* sections *Allophyllum* and *Aculeigerum* are morphologically distinctive, but both groups have narrow, tapered anthers that dehisce by small terminal pores, exclusively unbranched hairs, and frequently have pinnately lobed leaves.

9. *Cyphomandra* clade

ca. 50 spp., New World

Included taxa:

Solanum sect. *Pachyphylla* (Dunal) *Dunal* [genus *Cyphomandra* Sendtn.]*

Solanum sect. *Cyphomandropsis* Bitter*

Solanum sect. *Glaucophyllum* A. Child*

The association of these three sections and their relationship to *Solanum* have been controversial. From 1845 to 1995, *Cyphomandra* was recognized as a separate genus (Sendtner, 1845; Bohs, 1994, and references therein). However, molecular data establish that it is nested within *Solanum*, and all species of *Cyphomandra* were transferred to *Solanum* in 1995 (Bohs, 1995). *Solanum* sect. *Cyphomandropsis* was considered to be part of *Cyphomandra* by some workers (D'Arcy, 1972; Child, 1984b; Child & Lester, 2001), whereas others maintained this group in *Solanum* (Bitter, 1913b; Seithe, 1962; Gilli, 1970; Danert, 1970; Morton, 1976). Within *Solanum*, its subgeneric placement has been debated, with Seithe (1962) placing it in subgenus *Solanum* and Smith and Downs (1966) and Morton (1976) placing it in subgenus *Leptostemonum*. Most authors have considered *S. glaucophyllum* to belong to *Solanum* sect. *Cyphomandropsis*, but Child (1986) removed it to its own monotypic section and placed it in subgenus *Solanum*. Hunziker (2001) disagreed with this view on morphological grounds and placed it within *Solanum* subg. *Potatoe*. Morphological, cytological, and molecular studies have confirmed the close association of *Solanum* sections *Pachyphylla*, *Cyphomandropsis*, and *Glaucophyllum* (Morton, 1976; Moscone, 1992; Bohs, 2001; Bohs & Olmstead, 2001), and molecular data indicate that they form a distinct clade within *Solanum* whose close relatives are unclear (Fig. 1).

Species of the Cyphomandra clade are woody shrubs or trees that often have enlarged or elaborated anther connectives or dorsal anther surfaces. The synapomorphy that unites this group is the presence of very large chromosomes, which have been found in all species of the clade investigated to date.

10. Geminata clade

ca. 140 spp., mainly New World

Included taxa:

Solanum subg. *Solanum* pro parte

Solanum sect. *Geminata* (G. Don) Walp.*

Solanum sect. *Delitescens* Hunz. & Barboza*

Solanum sect. *Diamonon* (Raf.) A. Child*

Solanum subg. *Minon* Raf. pro parte

Solanum sect. *Holophylla* pro parte*

Solanum sect. *Pseudocapsicum*
(Moench) Bitter*

Although placed by D'Arcy (1972, 1991) in separate subgenera of *Solanum*, both morphological studies (Knapp, 2002) and the *ndh*F analyses confirm that section *Geminata* and section *Pseudocapsicum* are closely related. Both groups have mainly leaf-opposed inflorescences and often 1- to 2-foliate sympodial units. Yet other elements belong to the Geminata clade, such as *S. argentinum*, *S. delitescens*, and *S. havanense*. *Solanum argentinum* has been placed in section *Holophylla*, but this group is apparently polyphyletic, with at least part of the section belonging to the Dulcamaroid clade.

The systematic position of *S. delitescens* has been unclear. Knapp (2002) includes it in her treatment of *Solanum* sect. *Geminata*, but lists it under taxa of uncertain placement. Nee (1999) included it within the heterogeneous *Solanum* sect. *Holophylla* within subgenus *Solanum*. Hunziker and Barboza (in Hunziker, 2000) created the monotypic *Solanum* sect. *Delitescens* to accommodate this species and also placed it within subgenus *Solanum*. The *ndh*F data indicate that *Solanum* sections *Geminata*, *Pseudocapsicum*, and *Delitescens* are closely related to each other and are not allied with the morelloid species that make up the core of subgenus *Solanum*.

Likewise, the affinities of *Solanum havanense* have been uncertain. This species occurs in Cuba and Jamaica and, according to Knapp (2002), is allied to the Jamaican species *S. troyanum* Urb. Knapp (2002) excluded these two species from *Solanum* sect. *Geminata* and regarded them as an isolated lineage in *Solanum*, which she called the *S. havanense* species group (Knapp, 2002). Child (1998) created the monotypic *Solanum* sect. *Diamonon* to accommodate *S. havanense* and hypothesized that it may belong near section *Pseudocapsicum*. In the *ndh*F trees, *S. havanense* belongs to the *Geminata* clade along with members of *Solanum* sections *Geminata*, *Pseudocapsicum*, and *Delitescens*.

Characters that may unite the taxa of this clade include woody habit, unbranched to dendritically branched hairs, oblong anthers with large terminal pores, and fruits lacking stone cell aggregates.

11. Brevantherum clade

ca. 60 spp., New World

Included taxa:

Solanum subg. *Brevantherum* (Seithe)
D'Arcy pro parte [*Solanum* subg. *Minon*
pro parte in D'Arcy (1991)]

Solanum sect. *Brevantherum* Seithe*

Solanum sect. *Extensum* D'Arcy*

Solanum sect. *Lepidotum* Seithe*

Solanum sect. *Stellatigeminatum*
A. Child*

Solanum sect. *Cernuum* Carvalho
& G. J. Sheph.

Solanum subg. *Solanum* pro parte

Solanum sect. *Gonatotrichum*
Bitter*

For the most part, this clade consists of a number of morphologically similar groups that often have stellate hairs or lepidote scales, oblong anthers with large terminal pores, and green, yellow, or purple fruits. D'Arcy (1991) used the subgeneric name *Minon* to refer to an analogous group in *Solanum*, which, however, also included elements such as sections *Holophylla* and *Pseudocapsicum* that are here referred to different clades. Since the type species of subgenus *Minon* is *S. pseudocapsicum*, which belongs to the Geminata clade, the appropriate name for the Brevantherum clade at subgeneric rank would be *Solanum* subg. *Brevantherum*.

The sections of *Solanum* subg. *Brevantherum* are not well demarcated. The three members of *Solanum* sect. *Brevantherum* (*S. abutiloides*, *S. mauritianum*, *S. rugosum*) sampled in the *ndh*F trees do not form a monophyletic group, but additional data and sampling are needed to resolve relationships in the Brevantherum clade. There are a number of species that fall outside the traditional limits of the established sections listed above. One example is *Solanum inelegans*, placed by Nee (1999) in the polymorphic and ill-defined *Solanum* sect. *Holophylla* and evidently a member of the Brevantherum clade according to the *ndh*F data.

The odd group out from a morphological perspective is *Solanum* sect. *Gonatotrichum* (*S. adscendens*, *S. turneroides*, *S. deflexum*). Its placement here is surprising, because *Solanum* sect. *Gonatotrichum* has few of the characters listed above for the Brevantherum clade and has been thought to be more closely related to the Morelloid clade (D'Arcy, 1972, 1991; Nee, 1999; Child & Lester, 2001) or to *Solanum* sect. *Pseudocapsicum* of the Geminata clade (Hunziker, 2001). Molecular data indicate that *Solanum* sect. *Gonatotrichum* forms a distinct subclade within the Brevantherum clade (Fig. 1), but it clearly does not belong to the Morelloid clade. The names *S. adscendens* and *S. deflexum* may be synonymous (Nee, 1989, 1999; D'Arcy, 2001) but the two species exhibit a fair amount of sequence divergence in *ndh*F (1.0%) and are apparently allopatric (Bitter, 1912).

12. Leptostemonum clade

ca. 450 spp., worldwide

Includes all spiny sections and species groups except *Solanum* sect. *Aculeigerum* Seithe

Possibly includes *Solanum* sect. *Herposolanum* Bitter

Sampling to date includes at least 20 sections and 20 species groups *sensu* Whalen (1984)

This is the largest and most complex of the major clades of *Solanum* and encompasses the vast majority of species traditionally placed in *Solanum* subg. *Leptostemonum*. Data thus far indicate that all the species of *Solanum* that bear spines form a clade with the exception of section *Aculeigerum* mentioned above. Nearly all members of this group have stellate hairs as well as spines. The anthers are narrow and tapered with small terminal pores that do not enlarge into longitudinal slits. Much work is still needed to reveal the phylogenetic structure within the Leptostemonum clade and to interpret patterns of character evolution and biogeography within the group. A more detailed analysis of the Leptostemonum clade using *ndh*F and nuclear ITS sequence data is under way (L. Bohs, unpublished data) and will be summarized in a later publication.

The *ndh*F data indicate members of *Solanum* sections *Nemorense* (*S. nemorense*) and *Herposolanum* (*S. hoehnei*) may represent the basalmost branches in the Leptostemonum clade, but the bootstrap support for this grouping is low (51%). These taxa are similar to *Solanum* sect. *Aculeigerum* in that they have spines but lack stellate hairs. The placement of *Solanum* sect. *Herposolanum* has been particularly problematic; D'Arcy (1972, 1991) put it into *Solanum* subg. *Bassovia*, whereas Child (1983) suggested a relationship with *Solanum* sect. *Aculeigerum* (the Wendlandii/Allophyllum clade above) and provisionally placed it in *Solanum* subg. *Potatoe* (Child, 1990; Child & Lester, 2001). Whalen (1984) merged *Solanum* sections *Herposolanum* and *Nemorense* into his *S. nemorense* species group, which he considered to belong to *Solanum* subg. *Leptostemonum*. Nee (1999) included *Solanum* sect. *Aculeigerum* in section *Herposolanum* and regarded both as members of subgenus *Leptostemonum*. The *ndh*F data do not fully resolve these questions, but *Solanum* sections *Herposolanum* and *Nemorense* apparently do not belong to the Potato clade and are not closely related to section *Aculeigerum*.

Solanum sect. *Acanthophora* (*S. capsicoides*, *S. mammosum*) also appears to be relatively basal in the Leptostemonum clade. This group often has unbranched or weakly stellate hairs in addition to spines. These have been interpreted as being reduced stellate hairs (Nee, 1979), but a thorough examination of the ontogeny of hairs in this clade should be undertaken with a phylogenetic perspective to determine if these simple hairs represent an ancestral rather than derived state in the Leptostemonum group.

GENERAL RECOMMENDATION

This is not the last word on phylogenetic structure or evolutionary relationships in *Solanum*. The major clades identified here, although well supported from *ndh*F data, need to be corroborated by data from other genes. Additional sampling, especially from morphologically unusual, underrepresented, and/or putatively isolated groups, is needed to test the distinctiveness of the major *ndh*F clades and to ascertain the phylogenetic position of enigmatic taxa. For instance, no molecular data are available for the two species placed in *Solanum* sect. *Solanocharis* (Bitter) A. Child. The two species may not be closely related (M. Nee, pers. comm.), and they may not belong to *Solanum*. The type of the section is *S. albescens* (Britton) Hunz., which apparently has longitudinal anther dehiscence and has been regarded by some as belonging to the genera *Solanocharis*, *Poecilochroma*, or *Saracha* (Rusby, 1896; Bitter, 1918; M. Nee, pers. comm.). Molecular data will certainly aid in the interpretation of this puzzling group.

Morphological and biochemical characters also should be examined, especially in the light of molecular findings, in order to identify nonmolecular synapomorphies that support the *ndh*F clades. Taxonomic studies at lower levels to demarcate species limits are desperately needed for many subgeneric groups. Many nomenclatural issues also need careful clarification.

In light of these uncertainties, new formal taxonomic designations for infrageneric categories in *Solanum* are strongly discouraged without more extensive data and sampling. Progress will not be facilitated by the creation of yet more formal names that must be sifted through by all subsequent workers in the group. Informal names for species groups or clades (e.g., Whalen, 1984; Knapp, 1989, 2000, 2002; Bohs, 1994, 2001) are encouraged until enough data have accumulated to positively demarcate and define distinct evolutionary units within *Solanum*.

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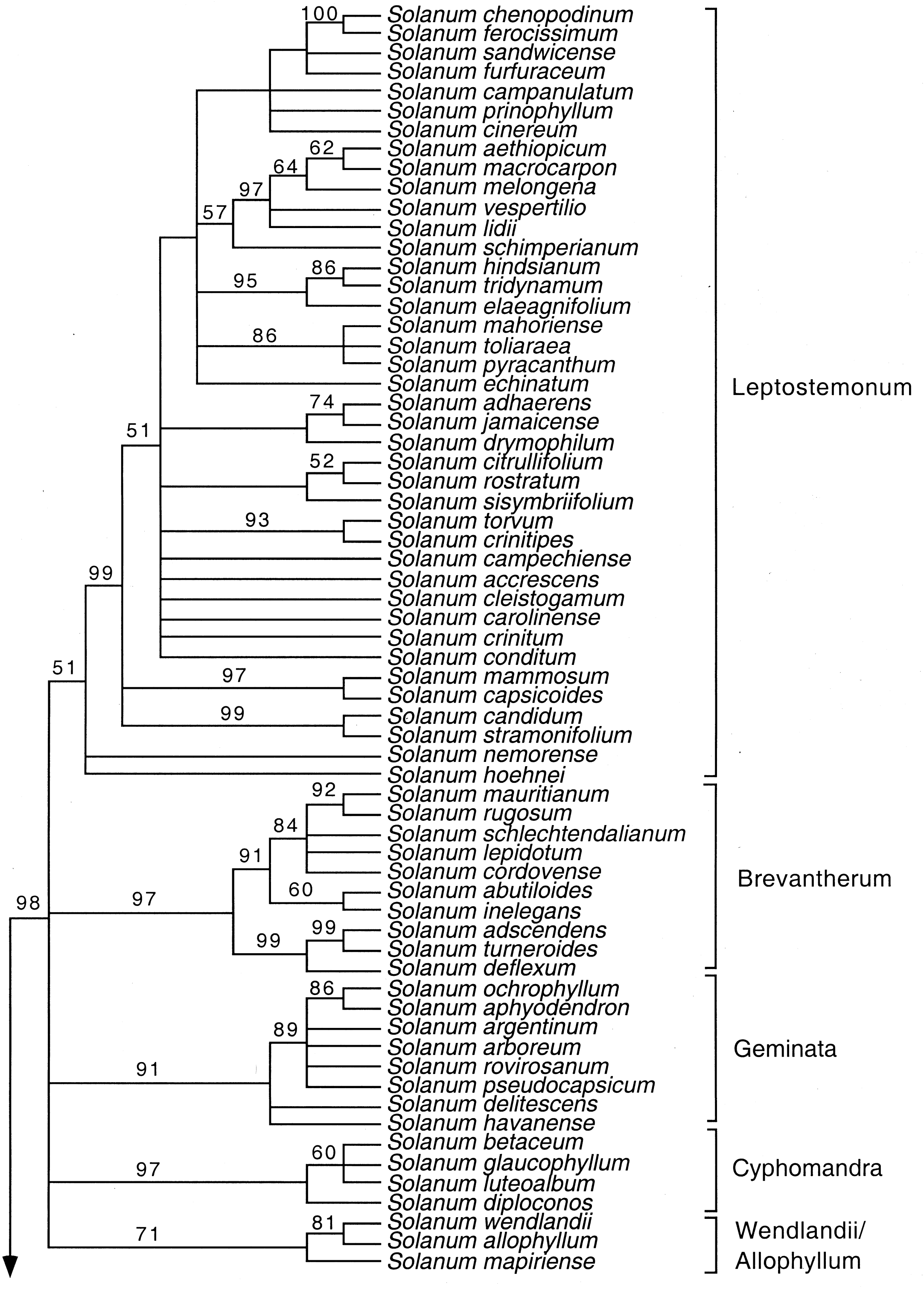

Figure 1. Strict consensus of 18,200 trees of 1053 steps from parsimony analysis of *ndh*F data. Numbers above branches are bootstrap values (500 replicates). Major clades in *Solanum* discussed in the text are labeled.

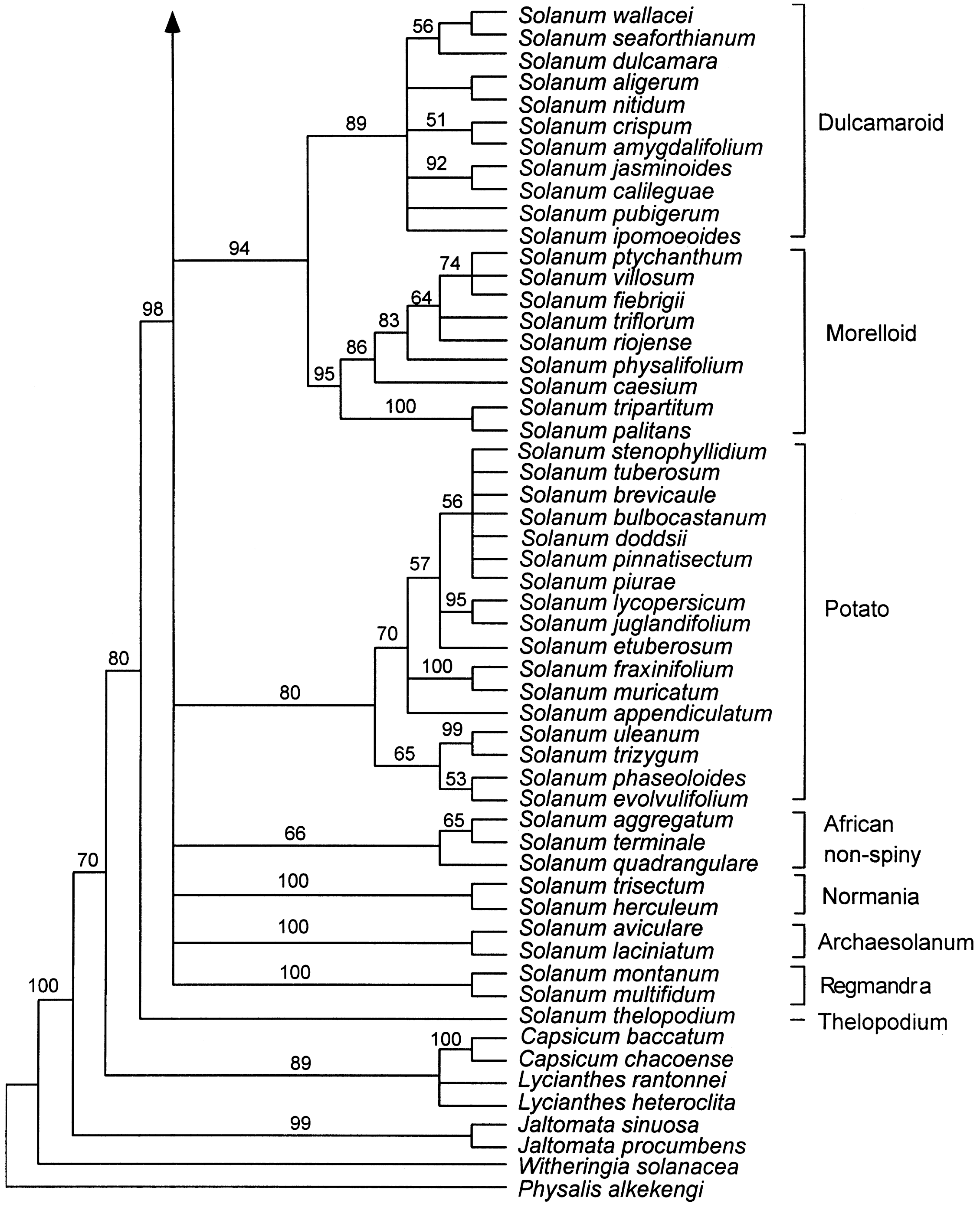

Figure 1 continued.