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A Three-Gene Phylogeny of the Genus *Solanum* (Solanaceae)

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ABSTRACT. *Solanum*, with approximately 1,500 species, is the largest genus in the Solanaceae and includes economically important species such as the tomato, potato, and eggplant. In part due to its large size and tropical center of diversity, resolving evolutionary relationships across *Solanum* as a whole has been challenging. In order to identify major clades within *Solanum* and to gain insight into phylogenetic relationships among these clades, we sampled 102 *Solanum* species and seven outgroup taxa for three DNA sequence regions (chloroplast *ndhF* and *trnT-F*, and nuclear *waxy*) and analyzed the data using parsimony and Bayesian methods. The same major *Solanum* clades were identified by each data partition, and the combined analysis provided the best resolved hypothesis of relationships within the genus. Our data suggest that most traditionally recognized *Solanum* subgenera are not monophyletic. The Thelopodium clade is sister to the rest of *Solanum*, which is split into two large clades. These two large clades are further divided into at least 10 subclades, for which informal names are provided and morphological synapomorphies are proposed. The identification of these subclades provides a framework for directed sampling in further phylogenetic studies, and identifies natural groups for focused revisionary work.

KEYWORDS: Eggplant, *ndhF*, potato, tomato, *trnT-F*, *waxy*.

Among seed plants, about 20 genera are thought to contain 1,000 or more species each (Frodin 2004). These ''giant genera'' present both problems and opportunities for plant systematists. Their size makes it difficult, if not impossible, for a single researcher to study them in their entirety, with the result that many have been ignored or avoided by taxonomists, lack full or even partial revisionary treatments, and have not been examined phylogenetically. On the other hand, giant genera represent unprecedented opportunities to investigate numerous morphological, biogeographical, developmental, and molecular questions within monophyletic and hyperdiverse groups. Some giant genera are artifacts of taxonomic neglect (''garbage groups''), whereas others are held together by striking synapomorphies (''key characters'') that may be indicative of rapid diversification. In order to make these large genera tractable for further study, their monophyly and component clades must be established and described. More focused studies can then be accomplished on smaller monophyletic groups within the giant genera.

Solanum is one such giant genus. Thought to encompass some 1,250 to 1,700 species, it is the largest genus in Solanaceae and within the top 10 most species-rich seed plant genera (Frodin 2004). *Solanum* is unique in the family in possessing anthers that open by terminal pores and flowers that lack the specialized calyx found in the related genus *Lycianthes*, which also has poricidal anther dehiscence. Species of *Solanum* occur on all temperate and tropical continents and exhibit remarkable morphological and ecological diversity. *Solanum* is arguably the most economically important genus of plants, containing familiar crop species such as the tomato (*S. lycopersicum*), potato (*S. tuberosum* L.), and eggplant (*S. melongena*), as well as many minor food plants and species containing poisonous or medicinally useful secondary compounds. Various species of *Solanum*, especially the tomato and potato, have served as model organisms for the investigation of many questions in cell and developmental biology and genetics, and currently *S. lycopersicum* is the focus of an entire-genome sequencing effort (http://www.sgn.cornell.edu/solanaceae-project/index.html).

Previous workers attempted to divide *Solanum* into two large groups, based either on presence vs. absence of prickles (Linnaeus 1753; Dunal 1813, 1816), oblong vs. tapered anthers (Dunal 1852; Bitter 1919), or stellate vs. non-stellate hairs (Seithe 1962). None of these systems is completely satisfactory for compartmentalizing morphological diversity within the genus. The later systems of D'Arcy (1972, 1991) recognized seven subgenera in *Solanum*, ranging in size from the monotypic subgenus *Lyciosolanum* to the subgenera *Solanum*, *Leptostemonum*, and *Potatoe*, each of which contain hundreds of species. Nee (1999), Child and Lester (2001), and Hunziker (2001) also provided infrageneric schemes for *Solanum* based on morphological characters and intuitive ideas of relatedness. Comparison of these classifications is difficult (Table 1); only Nee (1999) provided an explicit list of the species included in each of his subgenera, sections, and series, and his treatment is restricted primarily to New World taxa. The monophyly of many *Solanum* groups recognized by previous workers was examined by Bohs (2005) using

TABLE 1. Subgenera and sections of *Solanum* species sampled in this study according to taxonomic schemes of D'Arcy (1972, 1991, 1992) and Nee (1999). Modifications to D'Arcy's schemes indicated by: [a]Agra (2004). [b]Bohs (1990). [c]Symon (1981). [d]Child (1998).

Species	Subgenus of D'Arcy (1972, 1991, 1992)	Section of D'Arcy or other author, if indicated	Subgenus of Nee (1999)	Section of Nee (1999)
S. *abutiloides* (Griseb.) Bitter & Lillo	*Minon*	*Brevantherum*	*Solanum*	*Brevantherum*
S. *accrescens* Standl. & C. V. Morton	*Leptostemonum*	*Erythrotrichum*[a]	*Leptostemonum*	*Erythrotrichum*
S. *adhaerens* Roem. & Schult.	*Leptostemonum*	*Micracantha*	*Leptostemonum*	*Micracantha*
S. *adscendens* Sendtn.	*Solanum*	*Gonatotrichum*	*Solanum*	*Solanum*
S. *aethiopicum* L.	*Leptostemonum*	*Oliganthes*	*Leptostemonum*	*Melongena*
S. *aggregatum* Jacq.	*Lyciosolanum*	*Lyciosolanum*	Not treated	Not treated
S. *aligerum* Schltdl.	*Minon*	*Holophylla*	*Solanum*	*Holophylla*
S. *allophyllum* (Miers) Standl.	None	*Allophyllum*[b]	*Bassovia*	*Allophylla*
S. *amygdalifolium* Steud.	*Potatoe*	*Jasminosolanum*	*Solanum*	*Dulcamara*
S. *aphyodendron* S. Knapp	*Solanum*	*Geminata*	*Solanum*	*Holophylla*
S. *appendiculatum* Dunal	*Potatoe*	*Basarthrum*	*Solanum*	*Anarrhichomenum*
S. *arboreum* Dunal	*Solanum*	*Geminata*	*Solanum*	*Holophylla*
S. *argentinum* Bitter & Lillo	*Minon*	*Holophylla*	*Solanum*	*Holophylla*
S. *aviculare* G. Forst.	*Archaesolanum*	*Archaesolanum*	*Solanum*	*Archaesolanum*
S. *betaceum* Cav.	Genus *Cyphomandra*	*Pachyphylla*	*Bassovia*	*Pachyphylla*
S. *brevicaule* Bitter	*Potatoe*	*Petota*	*Solanum*	*Petota*
S. *bulbocastanum* Dunal	*Potatoe*	*Petota*	*Solanum*	*Petota*
S. *caesium* Griseb.	*Solanum*	*Solanum*	*Solanum*	*Solanum*
S. *calileguae* Cabrera	*Potatoe*	*Jasminosolanum*	*Solanum*	*Dulcamara*
S. *campanulatum* R. Br.	*Leptostemonum*	*Campanulata*	*Leptostemonum*	Probably *Melongena*
S. *campechiense* L.	*Leptostemonum*	Unclear	*Leptostemonum*	*Melongena*
S. *candidum* Lindl.	*Leptostemonum*	*Lasiocarpa*	*Leptostemonum*	*Lasiocarpa*
S. *capsicoides* All.	*Leptostemonum*	*Acanthophora*	*Leptostemonum*	*Acanthophora*
S. *carolinense* L.	*Leptostemonum*	*Lathryocarpum*	*Leptostemonum*	*Melongena*
S. *chenopodinum* F. Muell.	*Leptostemonum*	*Graciliflora*[c]	*Leptostemonum*	Probably *Melongena*
S. *cinereum* R. Br.	*Leptostemonum*	*Melongena*[c]	*Leptostemonum*	Probably *Melongena*
S. *citrullifolium* A. Braun	*Leptostemonum*	*Androceras*	*Leptostemonum*	*Melongena*
S. *clandestinum* Bohs	None	None	None	None
S. *cleistogamum* Symon	*Leptostemonum*	*Oliganthes*[c]	*Leptostemonum*	Probably *Melongena*
S. *conditum* C. V. Morton	*Leptostemonum*	Unclear	*Leptostemonum*	*Melongena*
S. *cordovense* Sessé & Moç.	*Minon*	*Extensum*	*Solanum*	*Brevantherum*
S. *crinitipes* Dunal	*Leptostemonum*	*Torva*	*Leptostemonum*	*Torva*
S. *crinitum* Lam.	*Leptostemonum*	*Crinitum*[d]	*Leptostemonum*	*Crinitum*
S. *crispum* Ruiz & Pav.	*Minon*	*Holophylla*	*Solanum*	*Holophylla*
S. *deflexum* Greenm.	*Solanum*	*Gonatotrichum*	*Solanum*	*Solanum*
S. *delitescens* C. V. Morton	*Minon*	*Holophylla*	*Solanum*	*Holophylla*
S. *diploconos* (Mart.) Bohs	Genus *Cyphomandra*	*Pachyphylla*	*Bassovia*	*Pachyphylla*
S. *drymophilum* O. E. Schulz	*Leptostemonum*	*Persicariae*	*Leptostemonum*	*Persicariae*
S. *dulcamara* L.	*Potatoe*	*Dulcamara*	*Solanum*	*Dulcamara*
S. *echinatum* R. Br.	*Leptostemonum*	*Leprophora*	*Leptostemonum*	Probably *Melongena*
S. *elaeagnifolium* Cav.	*Leptostemonum*	*Leprophora*	*Leptostemonum*	*Melongena*
S. *etuberosum* Lindl.	*Potatoe*	*Petota*	*Solanum*	*Petota*
S. *evolvulifolium* Greenm.	*Bassovia* or *Solanum*	Unclear	*Solanum*	*Herpystichum*
S. *ferocissimum* Lindl.	*Leptostemonum*	*Graciliflora*	*Leptostemonum*	Probably *Melongena*
S. *fiebrigii* Bitter	*Solanum*	*Solanum*	*Solanum*	*Solanum*
S. *fraxinifolium* Dunal	*Potatoe*	*Basarthrum*	*Solanum*	*Basarthrum*
S. *furfuraceum* R. Br.	*Leptostemonum*	*Oliganthes*[c]	*Leptostemonum*	Probably *Melongena*
S. *glaucophyllum* Desf.	*Solanum*	*Glaucophyllum*	*Bassovia*	*Cyphomandropsis*
S. *havanense* Jacq.	*Solanum*	*Diamonon*[d]	*Solanum*	*Holophylla*
S. *herculeum* Bohs	Genus *Triguera*		Not treated	
S. *hindsianum* Benth.	*Leptostemonum*	Unclear	*Leptostemonum*	*Melongena*
S. *hoehnei* C. V. Morton	*Leptostemonum*	*Nemorense*	*Leptostemonum*	*Herposolanum*
S. *inelegans* Rusby	Probably *Minon*	Unclear	*Solanum*	*Holophylla*
S. *ipomoeoides* Chodat & Hassl.	*Potatoe*	*Jasminosolanum*	*Solanum*	*Dulcamara*
S. *jamaicense* Mill.	*Leptostemonum*	*Eriophylla*	*Leptostemonum*	*Micracantha*
S. *juglandifolium* Dunal	*Potatoe*	*Petota*	*Solanum*	*Petota*
S. *laciniatum* Aiton	*Archaesolanum*	*Archaesolanum*	*Solanum*	*Archaesolanum*
S. *lepidotum* Dunal	*Minon*	*Lepidotum*	*Solanum*	*Brevantherum*
S. *lidii* Sunding	*Leptostemonum*	*Nycterium*	*Leptostemonum*	*Melongena*
S. *luteoalbum* Pers.	Genus *Cyphomandra*	*Cyphomandropsis*	*Bassovia*	*Cyphomandropsis*
S. *lycopersicum* L.	Genus *Lycopersicon*		Genus *Lycopersicon*	
S. *macrocarpon* L.	*Leptostemonum*	*Melongena*	*Leptostemonum*	*Melongena*

TABLE 1. Continued.

Species	Subgenus of D'Arcy (1972, 1991, 1992)	Section of D'Arcy or other author, if indicated	Subgenus of Nee (1999)	Section of Nee (1999)
S. mahoriensis D'Arcy & Rakot.	*Leptostemonum*	*Cryptocarpum*	*Leptostemonum*	Not treated
S. mammosum L.	*Leptostemonum*	*Acanthophora*	*Leptostemonum*	*Acanthophora*
S. mapiriense Bitter	None	*Allophyllum*[b]	*Bassovia*	*Cyphomandropsis*
S. mauritianum Scop.	*Minon*	*Brevantherum*	*Solanum*	*Brevantherum*
S. melongena L.	*Leptostemonum*	*Melongena*	*Leptostemonum*	*Melongena*
S. montanum L.	*Potatoe*	*Regmandra*	*Solanum*	*Regmandra*
S. muricatum Aiton	*Potatoe*	*Basarthrum*	*Solanum*	*Basarthrum*
S. nemorense Dunal	*Leptostemonum*	*Nemorense*	*Leptostemonum*	*Micracantha*
S. nitidum Ruiz & Pav.	*Minon*	*Holophylla*	*Solanum*	*Holophylla*
S. ochrophyllum Van Heurck & Müll. Arg.	*Solanum*	*Geminata*	*Solanum*	*Holophylla*
S. palitans C. V. Morton	*Solanum*	*Parasolanum*	*Solanum*	*Dulcamara*
S. physalifolium Rusby var. *nitidibaccatum* (Bitter) Edmonds	*Solanum*	*Solanum*	*Solanum*	*Solanum*
S. pinnatisectum Dunal	*Potatoe*	*Petota*	*Solanum*	*Petota*
S. prinophyllum Dunal	*Leptostemonum*	*Oliganthes*[c]	*Leptostemonum*	Probably *Melongena*
S. pseudocapsicum L.	*Minon*	*Pseudocapsicum*	*Solanum*	*Holophylla*
S. ptychanthum Dunal	*Solanum*	*Solanum*	*Solanum*	*Solanum*
S. pubigerum Dunal	*Minon*	*Holophylla*	*Solanum*	*Holophylla*
S. pyracanthos Lam.	*Leptostemonum*	*Oliganthes*	*Leptostemonum*	Probably *Melongena*
S. riojense Bitter	*Solanum*	*Episarcophyllum*	Not treated	Not treated
S. rostratum Dunal	*Leptostemonum*	*Androceras*	*Leptostemonum*	*Melongena*
S. rovirosanum Donn. Sm.	*Solanum*	*Geminata*	*Solanum*	*Holophylla*
S. rugosum Dunal	*Minon*	*Brevantherum*	*Solanum*	*Brevantherum*
S. sandwicense Hook. & Arn.	*Leptostemonum*	*Irenosolanum*	*Leptostemonum*	Not treated
S. schimperianum Hochst.	*Leptostemonum*	Unclear	*Leptostemonum*	Not treated
S. schlechtendalianum Walp.	*Minon*	*Extensum*	*Solanum*	*Brevantherum*
S. seaforthianum Andrews	*Potatoe*	*Jasminosolanum*	*Solanum*	*Dulcamara*
S. sisymbriifolium Lam.	*Leptostemonum*	*Cryptocarpum*	*Leptostemonum*	*Melongena*
S. stramonifolium Jacq.	*Leptostemonum*	*Lasiocarpa*	*Leptostemonum*	*Lasiocarpa*
S. thelopodium Sendtn.	None	None	*Bassovia*	*Pteroidea*
S. toliaraea D'Arcy & Rakot.	*Leptostemonum*	Unclear	*Leptostemonum*	Not treated
S. torvum Sw.	*Leptostemonum*	*Torva*	*Leptostemonum*	*Torva*
S. tridynamum Dunal	*Leptostemonum*	*Nycterium*	*Leptostemonum*	*Melongena*
S. triflorum Nutt.	*Solanum*	*Parasolanum*	*Solanum*	*Solanum*
S. tripartitum Dunal	*Solanum*	*Parasolanum*	*Solanum*	*Dulcamara*
S. trisectum Dunal	*Potatoe*	*Normania*	Not treated	Not treated
S. turneroides Chodat	*Solanum*	*Gonatotrichum*	*Solanum*	*Solanum*
S. uleanum Bitter	*Bassovia* or *Solanum*	*Pteroidea*	*Bassovia*	*Pteroidea*
S. vespertilio Aiton	*Leptostemonum*	*Nycterium*	*Leptostemonum*	*Melongena*
S. villosum Mill.	*Solanum*	*Solanum*	*Solanum*	*Solanum*
S. wendlandii Hook. f.	*Leptostemonum*	*Aculeigerum*	*Leptostemonum*	*Herposolanum*

molecular data from the chloroplast *ndhF* gene analyzed using cladistic methodology. Broad sampling from across a spectrum of *Solanum* species revealed that many of these infrageneric groups are not monophyletic. Bohs (2005) proposed an alternative classification for *Solanum* in which about 13 major lineages were identified and given informal clade names. The current study bolsters molecular support for these clades by adding sequence data from two other DNA sequence regions (*trnT-F* from the chloroplast genome and *waxy* from the nuclear genome) to that previously obtained from *ndhF*. Approximately 3,000 to 3,500 nucleotides of sequence were newly obtained for each of 109 taxa in order to obtain the best-resolved trees to date for the relationships of major clades within *Solanum*.

MATERIALS AND METHODS

Taxon Sampling. We sampled 102 *Solanum* species and seven outgroup species (Appendix 1) representing all seven *Solanum* subgenera and approximately 46 of the sections identified in D'Arcy (1972, 1991) and all three *Solanum* subgenera and many subgeneric groups recognized by Nee (1999; Table 1). To the extent possible, sampling followed Bohs (2005); 108 of the 120 species analyzed in Bohs (2005) are included here, as well as the recently described *S. clandestinum* (Nee et al. 2006). Seven *Solanum* species [*S. jasminoides* Paxton, *S. multifidum* Ruiz & Pav., *S. phaseoloides* Pol., *S. quadrangulare* L.f., *S. terminale* Forssk., *S. trizygum* Bitter, and *S. wallacei* (A. Gray) Parish] were excluded because they would not reliably amplify for one or more of the three genes examined in this study. Four taxa of the Potato clade (*S. doddsii* Correll, *S. piurae* Bitter, *S. stenophyllidium* Bitter, and *S. tuberosum* L.) were excluded because they formed a very closely related unresolved complex in Bohs (2005) that is under study by Dr. David Spooner of the University of Wisconsin, Madison. Outgroups representing seven species

TABLE 2. Descriptive statistics for each data set analyzed.

Data partition	Aligned sequence length	# parsimony informative characters	# MP trees	Tree length	CI	RI	# strongly supported nodes (≥ 90% BS) (parsimony)	Model selected	# strongly supported nodes (≥ 95% PP) (Bayesian)
ndhF	2,119	274	87,920	1,002	0.643	0.812	26	GTR+I+G	50
trnT-F	2,277	266	590,881	866	0.761	0.822	27	TVM+I+G	52
waxy	2,160	629	79,879	2,344	0.620	0.783	38	TVM+I+G	69
combined	6,556	1,169	21,017	4,278	0.644	0.788	56	Mixed	90

from four genera were selected from among lineages identified from previous studies as being most closely related to *Solanum (Capsicum*, *Jaltomata*, and *Lycianthes*; Olmstead et al. 1999; Bohs and Olmstead 2001). *Physalis alkekengi* served as a more distant outgroup to root the trees.

Molecular Methods. DNA was extracted from fresh or silica-dried leaves, or occasionally from herbarium specimens, using either a modified CTAB buffer method (Doyle and Doyle 1987) followed by cesium chloride density gradient centrifugation or phenol chloroform purification, or using the DNeasy plant mini extraction kit (Qiagen, Inc., Valencia, California).

PCR amplification for each gene region followed standard procedures described in Bohs and Olmstead (1997) for *ndhF*; in Taberlet et al. (1991), Bohs and Olmstead (2001), and Bohs (2004) for the *trnT-L* and *trnL-F* intergeneric spacer regions; and in Levin et al. (2005) for *waxy*. The *ndhF* region was amplified as a single fragment using primers 5′ and 3′. When possible, *trnT-F* and *waxy* were amplified as single fragments using primers a and f for *trnT-F* (Taberlet et al. 1991) and primers waxy F and waxy 2R for *waxy* (Levin et al. 2005). But, as necessary, overlapping fragments were amplified, sequenced, and subsequently assembled. In these cases, primers a with d, and c with f were used to amplify *trnT-F*, and primers waxy F with waxy 1171R and waxy 1058F with waxy 2R were used to amplify *waxy*.

PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Inc., Valencia, California). The University of Utah DNA Sequencing Core Facility performed sequencing on an ABI automated sequencer. Sequences were edited in Sequencher (Gene Codes Corp., Ann Arbor, Michigan), and all new sequences were submitted to GenBank (Appendix 1). Missing data comprised 0.0788% of the combined data matrix (457 bases out of a total of 579,891).

Sequence Alignment and Analysis. Sequence alignment for *ndhF* and the exon regions of *trnT-F* and *waxy* was straightforward and was performed visually using Se-Al (Rambaut 1996). Although *waxy* intron sequence alignment was more challenging, clearly recognizable sequence motifs that facilitated alignment were identified across all taxa. Similarly, most *trnT-L* spacer and *trnL* intron regions could be aligned with confidence. However, numerous sequence duplications have occurred in the *trnL-F* spacer between the 3′ *trnL* and *trnF* exons within the species surveyed and alignment in this region was extremely ambiguous. We included the 3′ *trnL* exon and the following 387 aligned nucleotides of sequence data in analyses, but excluded the remaining spacer – *trnF* exon region because it could not be aligned reliably. The aligned datasets and representative phylogenetic trees are available in TreeBASE (study number S1626).

PARSIMONY METHODS. Parsimony analyses were performed on each data set separately using PAUP*4.0b10 (Swofford 2002). All characters were weighted equally in analyses that implemented TBR branch swapping with 1,000 heuristic random addition replicates, each limited to 1,000,000 swaps per replicate. Gaps were treated as missing data. Bootstrapping (BS; Felsenstein 1985) was used to evaluate branch support with 1,000 random addition replicates and TBR branch swapping limited to 1,000,000 swaps per replicate. Each data set was further analyzed using the parsimony ratchet (Nixon 1999) as implemented in PAUPRat (Sikes and Lewis 2001) to search for shorter trees than were obtained in standard PAUP analyses. We followed the procedures for combining data sets outlined in Wiens (1998). After analyzing each data set (*ndhF*, *trnT-F*, *waxy*) independently, bootstrap values were used to identify strongly supported nodes (≥ 90% BS value) in each phylogeny. Taxa at strongly supported nodes that suggest different relationships were considered to be in conflict. The data were then combined and analyzed using the same methods outlined for the separate analyses. For those taxa in conflicting positions in the separate analyses, relationships were considered questionable in the combined analysis. Decay values (DI; Bremer 1988; Donoghue et al. 1992) were calculated for the separate and combined data sets as another method to assess nodal support. Constraints for decay value searches were generated using the program TreeRot (Sorenson 1999).

BAYESIAN METHODS. Prior to conducting Bayesian analyses, a general model of nucleotide evolution was selected for each data set using the AIC criterion identified in Modeltest 3.7 (Posada and Crandall 1998). MrBayes 3.1 (Huelsenbeck and Ronquist 2001) was used to analyze each data set separately prior to combining. For each data set, we ran four replicates of four Markov chains for 5,000,000 generations, each initiated from a random tree and sampled every 1,000 generations. All parameters from each analysis were visualized graphically and samples obtained prior to achieving stationary were discarded. Model parameters, likelihood values, and clade posterior probabilities (PP) from separate analyses of each data partition were compared before combining datasets to assess convergence in independent runs, and then summarized on a majority rule consensus tree (Huelsenbeck and Imennov 2002; Huelsenbeck et al. 2002).

RESULTS

Phylogenetic Analysis. Parsimony strict consensus and Bayesian majority rule consensus trees differed only in the degree of resolution; Bayesian tree topologies were more resolved than parsimony trees (Table 2). Clades with low posterior probability values in Bayesian analyses were often collapsed in the parsimony strict consensus trees. Unless otherwise noted, all figures and descriptions provided are based on strict consensus trees of parsimony analyses, which represent conservative estimates of *Solanum* phylogenetic relationships.

CHLOROPLAST DATA. Sequences of *ndhF* ranged in length from 2,077 to 2,119 bases, with an aligned length of 2,119 characters. Of these, 274 characters were parsimony informative. Parsimony analyses generated 87,920 most parsimonious trees of 1,002 steps, CI = 0.643, RI = 0.812. PAUPRat did not identify trees shorter than those obtained from the standard PAUP analyses. Modeltest selected the GTR + I + G model of evolution. In Bayesian analyses, graphical evaluation of all parameter values illustrated that the Markov chains attained stationary prior to generation 100,000 for the *ndhF* data. All trees obtained prior to generation 100,000 were eliminated as burn-in.

The length of *trnT-F* sequences varied between 1,442 and 1,712 bases, with an aligned length (after excluding the 3′ sequence region) of 2,277 characters, of which 266 were parsimony informative. The 590,881 most parsimonious trees had a length of 866 steps, CI = 0.761, RI = 0.822. PAUPRat did not find trees shorter than those obtained from the standard PAUP analyses. Modeltest selected TVM + I + G as the best fitting model of evolution. For the *trnT-F* data, graphical evaluation of all parameter values in Bayesian analyses illustrated that the Markov chains attained stationary prior to generation 500,000, so the first 500,000 trees were eliminated as burn-in.

NUCLEAR DATA. The *waxy* sequences ranged from 1,578 to 1,865 bases in length. Aligned sequence length was 2,160, and the data set contained 629 parsimony informative characters. The 79,879 most parsimonious trees had a length of 2,344 steps, CI = 0.620, RI = 0.783. PAUPRat did not identify trees shorter than those obtained from the standard PAUP analyses. The TVM + I + G model of evolution was selected by Modeltest. Graphical analyses of the results of Bayesian analyses illustrate that all parameter values attained stationary prior to generation 100,000 for the *waxy* data, and the first 100,000 trees were eliminated as burn-in.

COMBINED DATA. More nodes were resolved by combining the data than were obtained in any of the separate analyses, regardless of analytical method (Table 2). Parsimony analysis identified 21,017 trees of length 4,278, CI = 0.644, RI = 0.788. In the mixed model Bayesian analyses the first 100,000 trees were eliminated as burn-in.

Topological Conflict. With few exceptions, each DNA sequence region consistently identified the same major, well-supported clades comprising identical species groups, but relationships among these clades varied by data set, were often not strongly supported (BS values < 90%), or were unresolved, and thus cannot be considered conflicting under Wiens' (1998) criteria. More nodes are conflicting in the Bayesian analyses (cut off at ≤ 95% PP values), but posterior probabilities are known to be inflated relative to bootstrap values (Cummings et al. 2003; Erixon et al. 2003; Simmons et al. 2004) and are more prone to suggest strong support for incorrect phylogenetic hypotheses, particularly when the model of evolution is incorrectly specified (Douady et al. 2003). Therefore, to conservatively evaluate conflict among data sets, our discussion will be based on the topology of the parsimony strict consensus trees.

Apart from resolving a monophyletic *Solanum* (98% BS, 7 DI), the *trnT-F* strict consensus tree was poorly resolved at deep taxonomic levels within *Solanum* (Fig. 1). Clades with bootstrap support ≥ 90% were concentrated at the tips of the tree within species groups. As a result, Wiens' (1998) criterion did not identify strongly supported conflict at deep taxonomic levels between the *trnT-F* trees and *ndhF* or *waxy* topologies. Well-supported conflict between *trnT-F* and *waxy* involved sister group relationships among a few taxa within the Leptostemonum clade: the *trnT-F* data identified *S. adhaerens* and *S. citrullifolium* as sister species (93% BS, 3 DI; Fig. 1), and *S. jamaicense* and *S. rostratum* as sister species (100% BS, 5 DI; Fig. 1). Alternatively, *waxy* places *S. adhaerens* sister to *S. jamaicense* (100% BS, 14 DI; Fig. 2), and *S. citrullifolium* sister to *S. rostratum* (100% BS, 17 DI; Fig. 2). *Solanum adhaerens* and *S. jamaicense* share many morphological similarities and are placed together by Nee (1999) in *Solanum* sect. *Micracantha*. Likewise, *S. citrullifolium* and *S. rostratum* share a number of synapomorphies and have been placed in *Solanum* sect. *Androceras* (Whalen 1984; Nee 1999). Thus, the *waxy* tree is congruent with a suite of morphological characters used to delimit sections by Whalen (1984) and Nee (1999), lending support for the *waxy* topology in these regions of conflict.

More nodes were resolved by *ndhF* at deep taxonomic levels than by *trnT-F*, although few of these were strongly supported in the *ndhF* phylogeny (Fig. 3). The *ndhF* sequences provided strong support for the monophyly of *Solanum* exclusive of *S. thelopodium* (94% BS, 5 DI), and for the monophyly of the derived solanums including the Geminata, Cyphomandra, Brevantherum, and Leptostemonum clades plus the few unplaced taxa (96% BS, 6 DI). Most of these strongly supported clades were also present in the *trnT-F* and *waxy* trees (Fig. 1, 2), but typically with < 90% bootstrap support. The *ndhF* tree also provided strong support for the monophyly of many of the major clades, including the Morelloid (95% BS, 3 DI), the larger Morelloid + Dulcamaroid (95% BS, 4 DI), the

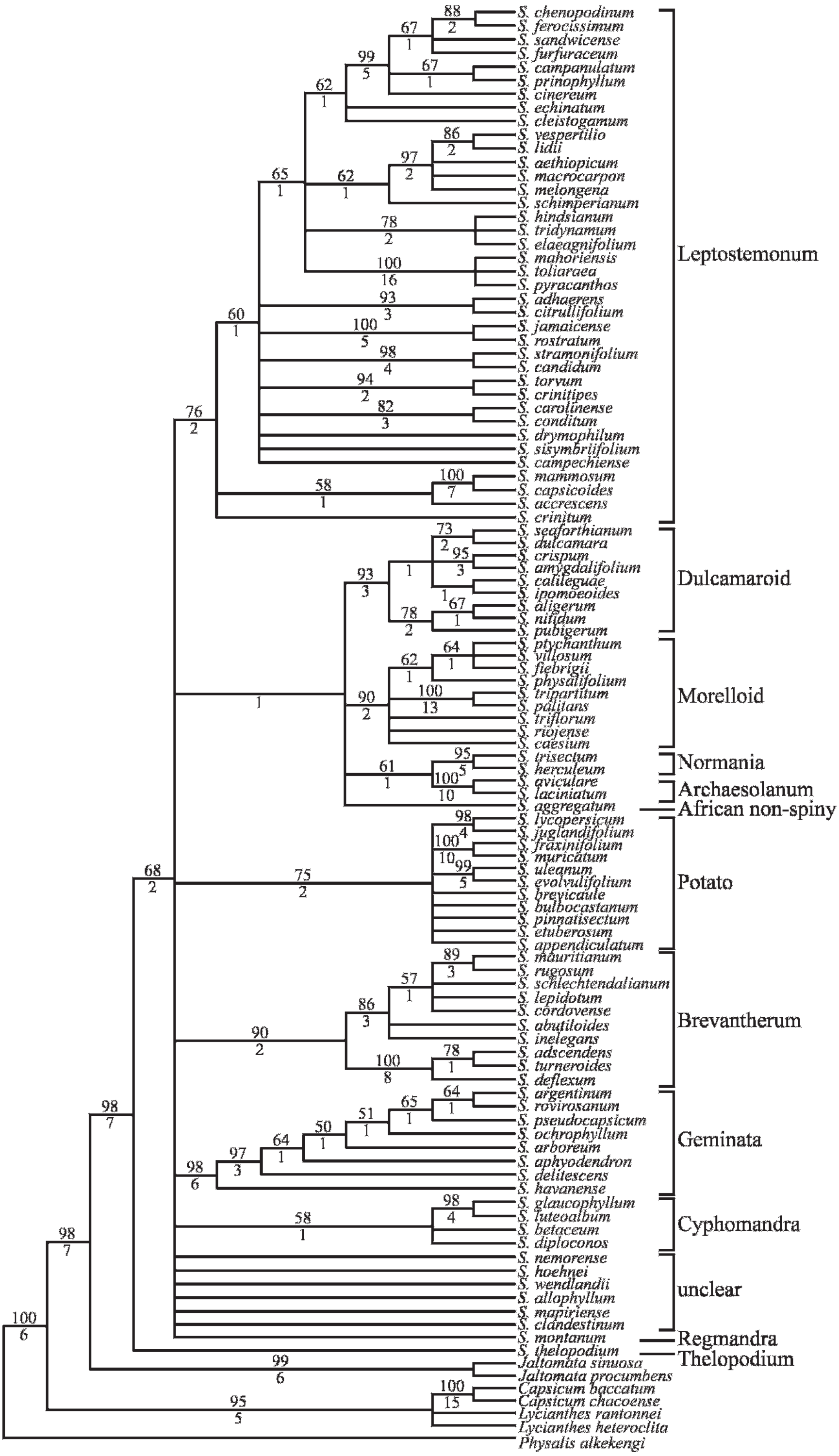

FIG. 1. Strict consensus of 590,881 most parsimonious trees obtained from the analysis of the *trnT-F* data alone. Numbers above branches are bootstrap values over 50% based on 1,000 random addition replicates; numbers below branches are decay values.

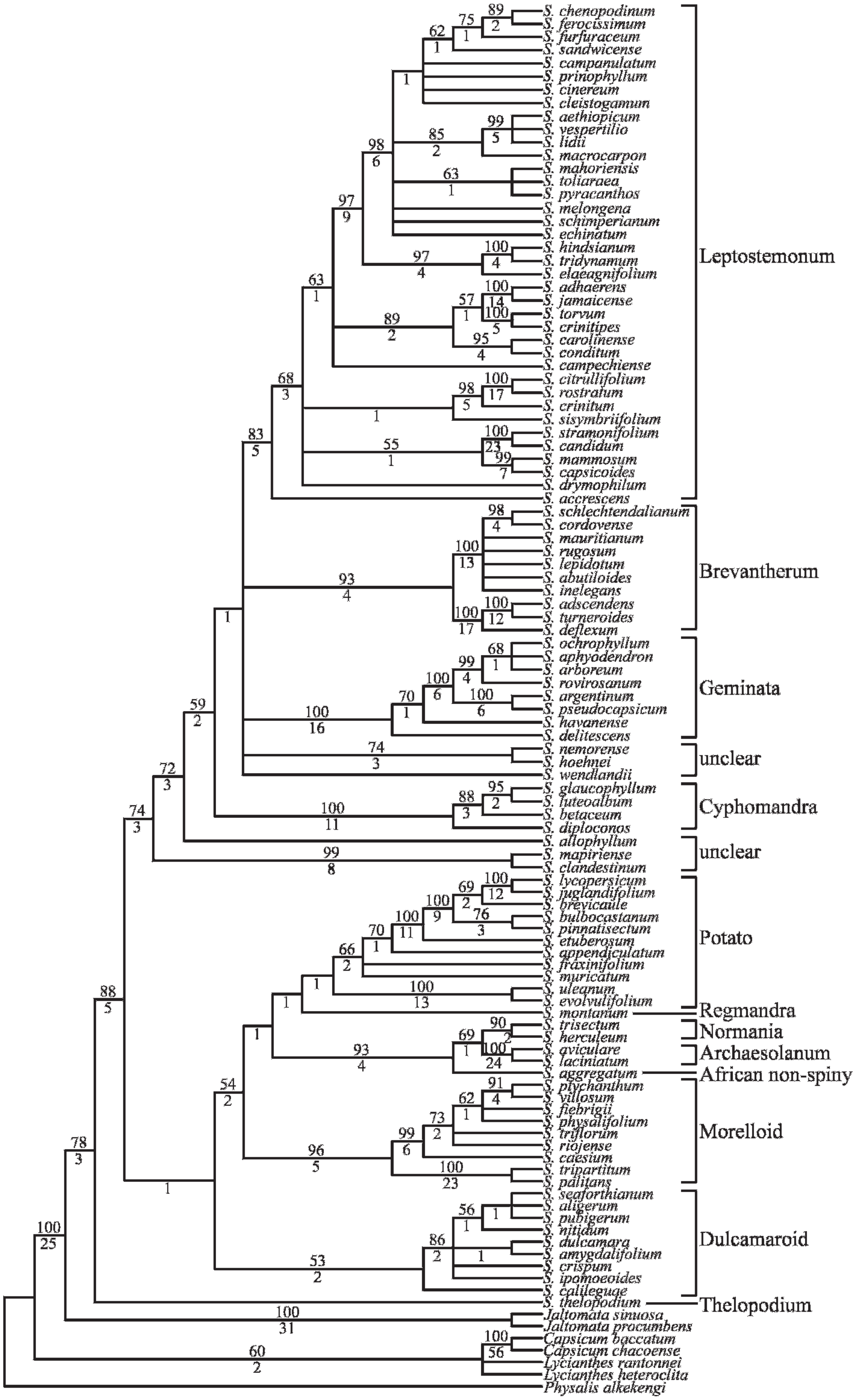

FIG. 2. Strict consensus of 79,879 most parsimonious trees obtained from the analysis of the *waxy* data alone. Numbers above branches are bootstrap values over 50% based on 1,000 random addition replicates; numbers below branches are decay values.

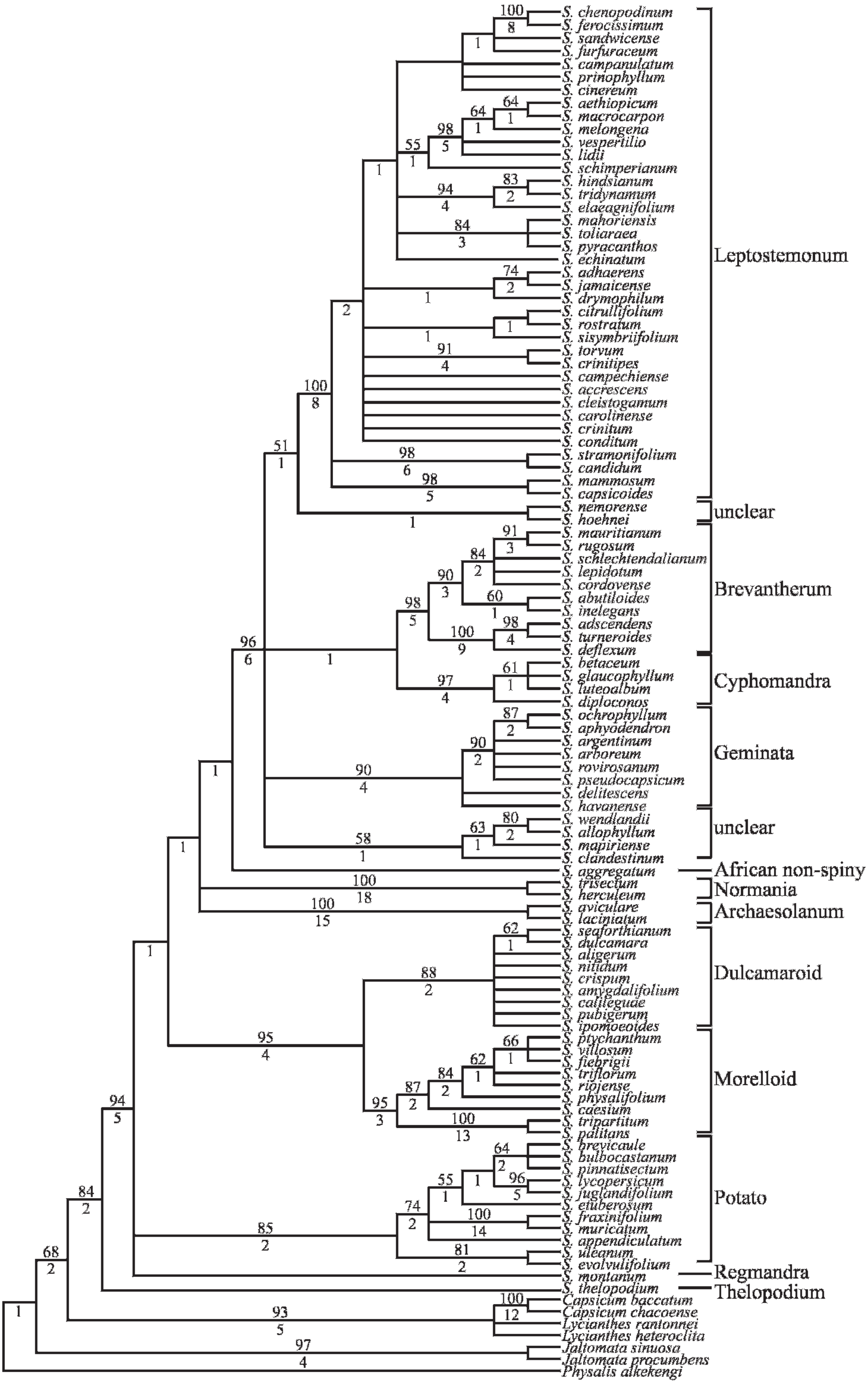

FIG. 3. Strict consensus of 87,920 most parsimonious trees obtained from the analysis of the *ndhF* data alone. Numbers above branches are bootstrap values over 50% based on 1,000 random addition replicates; numbers below branches are decay values.

Archaesolanum (100% BS, 15 DI), Normania (100% BS, 18 DI), Geminata (90% BS, 4 DI), and Leptostemonum (100% BS, 8 DI) clades.

The *waxy* strict consensus tree was better resolved than either the *trnT-F* or *ndhF* trees (Fig. 2), yet few nodes in the backbone of the tree had bootstrap values ≥ 90% in standard parsimony analyses. As in the *trnT-F* and *ndhF* trees (Fig. 1, 3), the same major clades were identified. The *waxy* sequences provided strong support for Jaltomata as sister to *Solanum* (100% BS, 25 DI), and for the Morelloid (96% BS, 5 DI), Archaesolanum (100% BS, 24 DI), Normania (90% BS, 2 DI), Cyphomandra (100% BS, 11 DI), Geminata (100% BS, 16 DI), and Brevantherum (93% BS, 4 DI) clades within *Solanum*. Sequences of *waxy* also suggested a sister group relationship among the African non-spiny, Archaesolanum, and Normania clades (93% BS, 4 DI). The *waxy* tree was better resolved at the tips than either *ndhF* or *trnT-F*, although many of the species-level relationships suggested by *waxy* were present in the *ndhF* and *trnT-F* results as well, but often with < 90% bootstrap support.

A number of species were of uncertain phylogenetic affinity in the separate analyses (Figs. 1–3). *Solanum nemorense* and *S. hoehnei* are placed weakly (51% BS, 1 DI) at the base of the Leptostemonum clade by *ndhF*, and were tentatively placed at the base, but included within the Leptostemonum clade by Bohs (2005). The *waxy* data unite these two species as sisters, but place them in a polytomy with *S. wendlandii* and the Geminata, Brevantherum, and Leptostemonum clades, whereas the species are unresolved within *Solanum* in the *trnT-F* analyses. The monophyly of the Allophyllum/Wendlandii group is also unclear. *NdhF* identifies *S. wendlandii, S. allophyllum, S. mapiriense*, and the recently described *S. clandestinum* as a clade, but with low bootstrap support (58%, 1 DI; Fig. 3). The *waxy* data identifies *S. clandestinum* as sister to *S. mapiriense* (99% BS, 8 DI; Fig. 2), but *S. allophyllum* and *S. wendlandii* do not emerge as sister taxa in analysis of *waxy* alone, and the position of *S. allophyllum, S. clandestinum, S. mapiriense, and S. wendlandii* are unresolved in the *trnT-F* analysis (Fig. 1).

Combined Analysis. The strict consensus tree inferred from the combined data was more resolved at all taxonomic levels (Fig. 4) than were those based on the separate analyses, and begins to provide an indication of relationships among many of the major *Solanum* clades. These data identify a monophyletic *Solanum* (99% BS, 13 DI), and place *S. thelopodium* sister to the rest of the genus. The *ndhF* data resolved the *Capsicum*/*Lycianthes* clade as sister to *Solanum*, but all other data partitions, including the combined data, identified *Jaltomata* as the sister genus to *Solanum*. *Solanum* comprises three major clades, treated here informally: 1) *S. thelopodium*, which is sister to the rest of *Solanum*; 2) Clade I, that includes the Regmandra and African non-spiny species and the Potato, Archaesolanum, Normania, Morelloid, and Dulcamaroid clades; and 3) Clade II, that includes the Cyphomandra, Geminata, Brevantherum, and Leptostemonum clades, as well as the species with unclear affinities described above. Clades I and II can be further subdivided into at least 10 subclades, mostly corresponding with the informal clades recognized in Bohs (2005) that will be discussed below.

DISCUSSION

Relationships of Subgenera Sensu D'Arcy & Nee. For various reasons, it is difficult to comprehensively compare widely-used morphology-based taxonomic schemes of previous *Solanum* systematists with the structure proposed here. D'Arcy (1972) listed only the type species for each section and did not provide morphological definitions for his subgenera and sections, so placing a non-type species in his classification is difficult. Nee (1999) provides an explicit list of species thought to belong to his subgenera and sections, but his treatment is restricted mostly to New World taxa. Hunziker (2001) summarizes *Solanum* classification, but his system is based primarily on previous schemes of D'Arcy and Nee.

Nonetheless, it can safely be stated that the major *Solanum* clades recognized here and in Bohs (2005) differ substantially from the subgenera of D'Arcy (1972, 1991) and Nee (1999). Of D'Arcy's seven subgenera, only subgenus *Leptostemonum* is largely represented as a monophyletic group in the trees based on molecular data. Nee (1999) recognizes only three broadly-defined *Solanum* subgenera (subgenera *Solanum*, *Bassovia*, and *Leptostemonum*). Of these, only *Leptostemonum* emerges largely intact in the analyses presented here. We submit that our proposed scheme, recognizing 12 to 15 major clades within *Solanum*, represents our best current estimate of natural evolutionary groups within the genus.

D'Arcy (1972, 1991) also recognized approximately 60–70 sections below the subgeneric level in *Solanum*. In many cases, these groups are recognized at the rank of series or subseries in Nee (1999), but detailed comparisons among these two systems are difficult, if not impossible. Table 1 attempts to compare the taxonomic disposition of the species sampled here in the systems of both D'Arcy (1972, 1991, 1992) and Nee (1991), but at best this is an approximation. In the following

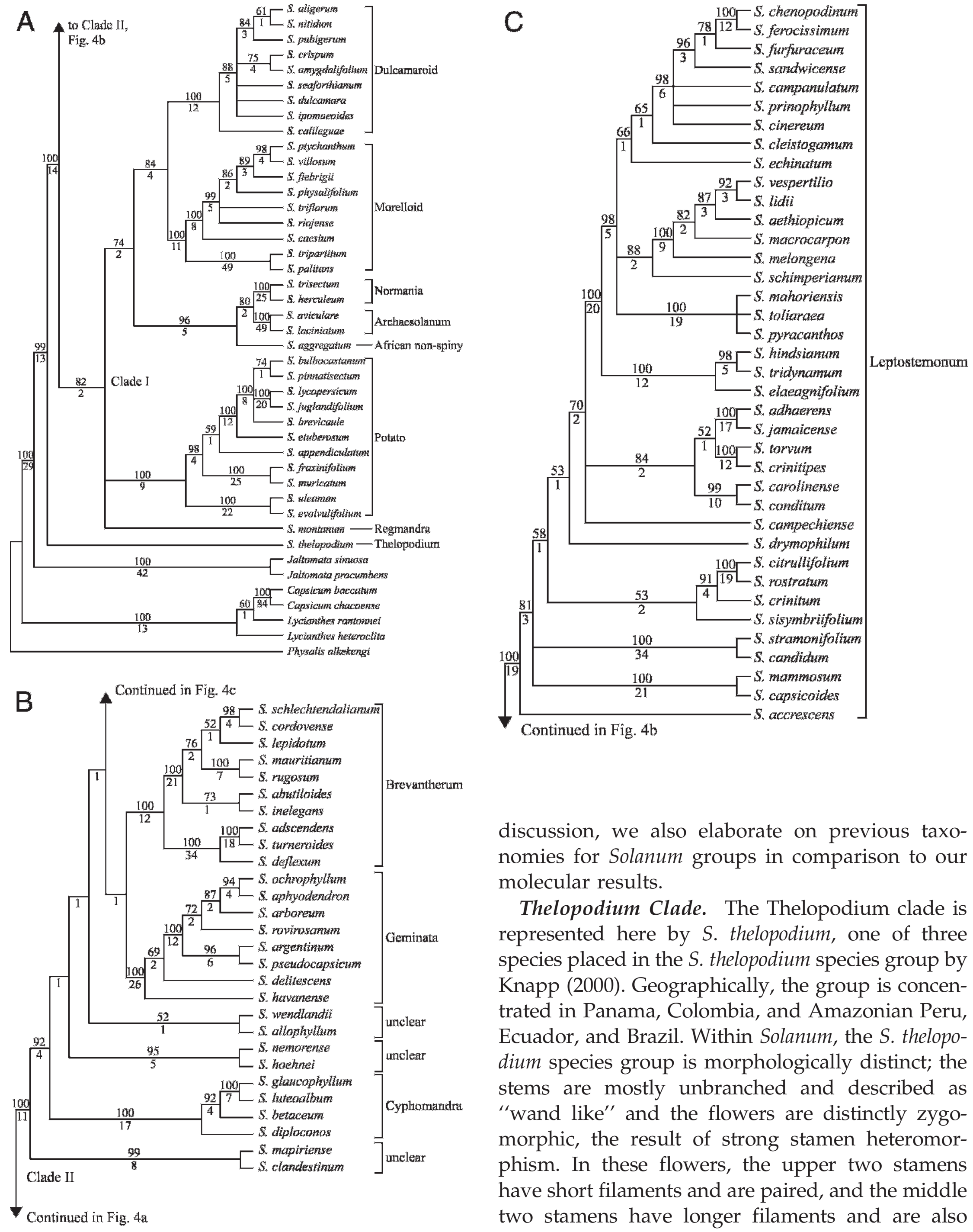

FIG. 4. Strict consensus of 21,017 most parsimonious trees obtained from the combined analysis of the *trnT-F*, *ndhF*, and *waxy* data. Numbers above branches are bootstrap values over 50% based on 1,000 random addition replicates; numbers below branches are decay values. The major clades discussed in the text are labeled.

discussion, we also elaborate on previous taxonomies for *Solanum* groups in comparison to our molecular results.

Thelopodium Clade. The Thelopodium clade is represented here by *S. thelopodium*, one of three species placed in the *S. thelopodium* species group by Knapp (2000). Geographically, the group is concentrated in Panama, Colombia, and Amazonian Peru, Ecuador, and Brazil. Within *Solanum*, the *S. thelopodium* species group is morphologically distinct; the stems are mostly unbranched and described as ''wand like'' and the flowers are distinctly zygomorphic, the result of strong stamen heteromorphism. In these flowers, the upper two stamens have short filaments and are paired, and the middle two stamens have longer filaments and are also paired. The lowermost stamen is the longest due to its long filament and anther, both of which are the largest within the flower. Parsimony analyses consistently place *S. thelopodium* as sister to the rest of *Solanum*; however, Bayesian analyses (not shown), which should account for long-branch attraction, place *S. thelopodium* in a basal polytomy with Clades I and II. In either case, the molecular data separate *S. thelopodium* from the rest of the sampled *Solanum* species. *Solanum thelopodium* was placed in section *Pteroidea* by Nee (1999), but our data show that *S. thelopodium* is distant from *S. uleanum*, which is placed firmly in section *Pteroidea* in the latest revision of the section (Knapp and Helgason 1997). Ideally, the two remaining species from the *S. thelopodium* species group (Knapp 2000) should be analyzed in a phylogenetic context to test the monophyly of the group and to assess the relative levels of support for relationships between the *S. thelopodium* species group and other *Solanum* clades. Unfortunately, silica-dried material of these species has not yet been obtained in the field and extracts from herbarium specimens have failed to amplify. Until these species can be incorporated into phylogenetic analyses, their shared morphological characters are sufficiently convincing to suggest a close relationship among the three species.

Clade I. REGMANDRA CLADE. *Solanum montanum*, the type species of sect. *Regmandra* (D'Arcy 1972), is included here to represent the section that comprises approximately 10 species. Geographically, species in sect. *Regmandra* are restricted to Peru and Chile. Although the higher-level taxonomic position of the section has been unstable (D'Arcy 1972, 1991; Nee 1999; Child and Lester 2001; Hunziker 2001), sect. *Regmandra* is cohesive morphologically; the plants are low herbs with slightly lobed to highly pinnately dissected, somewhat thickened leaves, often with decurrent, winged petioles. The flowers of *S. montanum* and *S. multifidum* have nearly rotate corollas and markedly enlarged stigmas. *Solanum montanum* has been described as bearing tubers (Dunal 1852; Macbride 1962). Many individuals of *S. montanum* have enlarged stem bases, but they are not homologous to the true tubers found in species of the Potato clade (J. Bennett, pers. comm.). The molecular data do not support a close relationship between *S. montanum* and the tuber-bearing members of *Solanum* (the derived members of the Potato clade), but the *waxy* and combined data do provide weak support for a sister group relationship between *S. montanum* and the entire Potato clade. However, these results be may be an artifact of sampling, and should be considered preliminary until additional species from within sect. *Regmandra* can be sampled and the higher-level relationship among the Regmandra clade and other identified *Solanum* clades can be explored.

POTATO CLADE. The strongly supported Potato clade (100% BS, 9 DI, 100% PP) includes most sections from D'Arcy's (1972) subgenus *Potatoe* as well as representatives from his subgenus *Bassovia*. Other species that have been treated in subgenus *Potatoe* are removed to a separate Dulcamaroid clade (discussed below). The Potato clade is a large, mainly South American group of herbaceous to weakly woody, often scandent plants, most with compound leaves, and some with rhizomes or tubers. The tuber-bearing species, here represented by *S. bulbocastanum*, *S. pinnatisectum*, and *S. brevicaule*, are derived within the clade and are closely related to tomato (*S. lycopersicum*) and its wild relative *S. juglandifolium*, consistent with results of numerous previous studies (Olmstead and Palmer 1992, 1997; Spooner et al. 1993; Bohs and Olmstead 2001; Bohs 2005). A close affinity between *Solanum* sect. *Etuberosum*, here represented by *S. etuberosum*, and the tuber-bearing potatoes is also widely accepted (Lindley 1835; Contreras-M. and Spooner 1999). Species in sects. *Anarrhichomenum* and *Basarthrum* (represented here by *S. appendiculatum*, *S. fraxinifolium*, and *S. muricatum*) have been treated within subgenus *Potatoe* (D'Arcy 1972, 1991; Child and Lester 2001), a relationship supported in these analyses. The sister relationship between *S. fraxinifolium* and *S. muricatum*, the two species sampled from sect. *Basarthrum*, is also consistent with previous taxonomic opinion (Anderson 1979; Anderson and Jansen 1998).

Solanum uleanum (sect. *Pteroidea*; Knapp and Helgason 1997) is resolved as sister to *S. evolvulifolium* (sect. *Herpystichum*; Nee 1999) in this study, and both taxa are sister to the remaining species of the Potato clade in this study and in earlier analyses of *ndhF* sequences alone (Bohs 2005). *Solanum* sect. *Pteroidea* comprises a group of 12 species of understory herbs and vines with apparently axillary inflorescences. The plants often climb using adventitious roots. Although a close relationship between sect. *Pteroidea* and the Potato clade was not suggested by earlier workers (Knapp and Helgason 1997), the generally scandent habit, adventitious roots, and pinnatifid leaves of some species in sect. *Pteroidea* are also typical of many members of the Potato clade. Similarly, *S. evolvulifolium* is a vine or scandent shrub with nodal roots.

NORMANIA – ARCHAESOLANUM – AFRICAN NON-SPINY CLADE. A strongly supported relationship (96% BS, 5 DI, 100% PP) among these taxa is surprising as no obvious morphological synapomorphies or biogeographic distributional patterns exist to unite them. An identical relationship is suggested by the *waxy* data when analyzed alone (93% BS, 4 DI, 100% PP; Fig. 2), and the *trnT-F* data resolve the Normania and Archaesolanum clades as sister to each other (61% BS, 1 DI, 94% PP; Fig. 1), but *S. aggregatum* (the African non-spiny species) is unresolved within a larger clade including the Dulcamaroid and Morelloid clades.

The relationship among all three taxa is unresolved by the *ndhF* data alone (Fig. 3). Each of these lineages will be discussed separately.

The strongly-supported Archaesolanum clade (100% BS, 49 DI, 100% PP) samples two of the approximately eight species treated in sect. *Archaesolanum* (Symon 1994). This section is restricted to New Guinea, Australia, Tasmania, and New Zealand, and includes semi-woody shrubs with highly variable leaf morphology, flowers with relatively long filaments, and fruits that typically contain numerous and conspicuous stone cell granules. Section *Archaesolanum* is best defined cytologically; the species are aneuploids with a base chromosome number of $n = 23$, unlike the rest of *Solanum*, in which the base chromosome number is $n = 12$. *Solanum* taxonomists have emphasized this feature, and most have placed species in the Archaesolanum clade in their own subgenus or section (Marzell 1927; Danert 1970; D'Arcy 1972, 1991; Symon 1994; Nee 1999; Child and Lester 2001). Section *Archaesolanum* also has been resolved as a well-supported clade in previous analyses of DNA sequence data (Bohs and Olmstead 2001; Bohs 2005), although the higher-level relationships between these species and other clades was unclear. Our combined analysis places this clade sister to the Normania clade with reasonable support valuables (80% BS, 2 DI, 98% PP). This relationship is also supported in the separate analyses of *trnT-F* and *waxy* alone (Figs. 1, 2), and in the Bayesian analysis of *ndhF* data (not shown); however, no obvious macromorphological characters suggest a close relationship between the Archaesolanum and Normania clades.

The strongly supported Normania clade (100% BS, 25 DI, 100% PP) samples two of the three species that have been alternatively segregated into the genera *Normania* and *Triguera* (reviewed in Francisco-Ortega et al. 1993) or treated within *Solanum* subgenus *Potatoe* (D'Arcy 1972; Child 1990). *Solanum trisectum* [formerly *Normania triphylla* (Lowe) Lowe] is one of two species of sect. *Normania*, whereas *S. herculeum* [formerly *Triguera osbeckii* (L.) Willk.] is the sole representative of the monotypic genus *Triguera*. Geographically, members of the Normania clade are native to northwestern Africa, the adjacent Iberian Peninsula, and the Macaronesian islands. A close relationship between *Normania* and *Triguera* was suggested by similarities in seed coat morphology, the slightly zygomorphic corollas, leafy calyces, horned anthers, and pollen colpi joined at the pores (Francisco-Ortega et al. 1993; Bohs and Olmstead 2001). Francisco-Ortega (1993) argued that these differences were sufficient to segregate *Normania* from *Solanum*, in a position near *Triguera*, particularly since the unusual seed coat morphology observed in these taxa was not present in other surveyed species from subgenus *Potatoe*. Our data support a close relationship among the *Normania* and *Triguera* species but resolve these taxa well within *Solanum* and sister to the Archaesolanum clade, a relationship consistent with Bohs and Olmstead (2001) and Bohs (2005). Based on these results, a survey of seed coat morphology within the more closely related Archaesolanum and African non-spiny clades, rather than in subgenus *Potatoe*, may reveal meaningful insights into the evolution of this character within *Solanum*.

The African non-spiny clade is represented in these analyses by *S. aggregatum*. Bitter (1917) and Seithe (1962) treated *S. aggregatum* as the monotypic subgenus *Lyciosolanum*, citing the elongate stamen filaments and localized distribution in extreme southern Africa as unique within *Solanum* (D'Arcy 1972). Bohs (2005) recovered *S. aggregatum* within a larger clade that also included *S. terminale* of sect. *Afrosolanum* and *S. quadrangulare* of sect. *Quadrangulare.* We were unable to obtain *waxy* sequences for *S. terminale* and *S. quadrangulare*, and relationships among these species based on the *trnT-F* sequence region were unresolved (not shown). The African non-spiny *Solanum* clade is poorly characterized both morphologically and molecularly and needs careful examination to elucidate its taxonomic limits and closest relatives within *Solanum*.

MORELLOID – DULCAMAROID CLADE. Bohs' (2005) analysis of *ndhF* data identified a close relationship between the Morelloid and Dulcamaroid clades (94% BS support). Our combined data also suggest a sister group relationship between these two groups, although the support values in the combined analysis are lower (84% BS, 4 DI, 100% PP) than in the analysis of *ndhF* alone (95% BS, 4 DI, 100% PP; Fig. 3). We retain the informal Morelloid - Dulcamaroid clade name, and discuss each separately below.

The strongly supported Morelloid clade (100% BS, 11 DI, 100% PP) includes representatives from the predominantly New World sects. *Solanum*, *Episarcophyllum*, *Campanulisolanum*, and *Parasolanum*. Section *Solanum* can be weedy and has a worldwide distribution, but its greatest species diversity is in the New World. The group is morphologically plastic, and taxonomy is complicated by polyploidy and natural hybridization. Section *Campanulisolanum* (represented here by *S. fiebrigii*) includes two species with campanulate corollas (Barboza and Hunziker 2005). These have been variously treated as members of sect. *Solanum* (D'Arcy 1972; Edmonds 1972, 1977, 1978; Edmonds and Chweya 1997), differentiated as sect. *Campa-*

nulisolanum (Bitter 1912; Morton 1976; Barboza and Hunziker 2005), or recognized as a subsection within sect. *Solanum* (Child 1998; Nee 1999). In our analyses, *S. fiebrigii* is nested within a group of species belonging to sect. *Solanum* (*S. ptychanthum*, *S. villosum*, and *S. physalifolium*). Recognition of sect. *Campanulisolanum* would thus render sect. *Solanum* paraphyletic. However, more species from the Morelloid clade need to be examined in a phylogenetic context before the relationships of sections within this clade are known with certainty.

The circumscription of other groups or sections within the Morelloid clade has been unclear and differs among *Solanum* taxonomists. For instance, Del Vitto and Petenatti (1999) include *S. riojense* in sect. *Episarcophyllum*, a group of high elevation, mostly herbaceous plants with somewhat fleshy leaves. They exclude *S. caesium* from sect. *Episarcophyllum* and place it in sect. *Solanum*. Nee (1999) demotes sect. *Episarcophyllum* to a subsection within sect. *Solanum* and includes *S. caesium* within it; *S. riojense* is not included in his classification. Regardless of its circumscription, the species of sect. *Episarcophyllum* are closely related to sect. *Solanum* and are expected to belong to the Morelloid clade.

Similarly, three species defined by Child (1984a) as sect. *Parasolanum* belong to the Morelloid clade, but the molecular data cast doubt on the circumscription and monophyly of the section. *Solanum triflorum*, the type species for sect. *Parasolanum*, does not comprise a clade with *S. tripartitum* and *S. palitans*, the other sampled representatives of the section. Analyses of *waxy* and *trnT-F* sequences from *S. radicans* and *S. corymbosum*, two other sect. *Parasolanum* species, place these taxa in a clade together with *S. tripartitum* and *S. palitans* (data not shown). Section *Parasolanum* may be made monophyletic by removing *S. triflorum* from the group; however, a new type and sectional name must be designated. Nee (1999) did not consider *S. triflorum* to be closely related to *S. tripartitum* and *S. palitans* and placed *S. triflorum* in sect. *Solanum*, a view supported by the molecular trees. However, his placement of *S. tripartitum* and *S. palitans* in sect. *Dulcamara* (Dulcamaroid clade) is not supported by the data presented here.

Members of the strongly supported Dulcamaroid clade (100% BS, 12 DI, 100% PP) have a worldwide distribution. Many species in this clade have a vining habit and climb by means of twining petioles and many, if not most, have pedicels inserted on small platforms or sleeves within the inflorescence. The sampled species include members of sects. *Dulcamara* and *Jasminosolanum*, thought by D'Arcy (1972) to be related to the potatoes, and sect. *Holophylla*, which D'Arcy (1972) considered to be related to members of sect. *Brevantherum* (Brevantherum clade) and Nee (1999) considered to be related to sect. *Geminata* (Geminata clade). Although none of the sections *Dulcamara*, *Jasminosolanum*, or *Holophylla* are monophyletic in the phylogeny, the relationships among the species of the Dulcamaroid clade are poorly resolved and none of the species groups identified within the clade have bootstrap values > 90%. All sampled members of sects. *Dulcamara* and *Jasminosolanum* (*S. calileguae*, *S. ipomoeoides*, *S. dulcamara*, *S. seaforthianum*, and *S. amygdalifolium*) are resolved within the Dulcamaroid clade. However, sect. *Holophylla* is grossly polyphyletic, with representatives of the group emerging in disparate clades in the molecular analyses. For example, species of the *S. nitidum* group (*S. crispum* and *S. nitidum*; Knapp 1989) as well as *S. pubigerum* and *S. aligerum* belong to the Dulcamaroid clade, whereas *S. argentinum* is placed within the Geminata clade. Knapp (1989) recognized that sect. *Holophylla* was not monophyletic and began a revision of the section focusing on the *S. nitidum* species group, which was thought to be a natural, monophyletic lineage. The two sampled species from this group, *S. crispum* and *S. nitidum*, are placed within the Dulcamaroid clade, but are not sister taxa in the molecular trees.

Clade II. CYPHOMANDRA CLADE. Species of the Cyphomandra clade are neotropical woody shrubs or small trees with unusually large chromosomes and high nuclear DNA content (Bohs 1994, 2001). They have been traditionally placed into two to three sections of *Solanum* (sects. *Pachyphylla*, *Cyphomandropsis*, and *Glaucophyllum*) and sect. *Pachyphylla* was formerly recognized as the separate genus, *Cyphomandra*. Although most workers have considered *S. glaucophyllum* to belong in sect. *Cyphomandropsis*, others (e.g., Child 1986; Child and Lester 2001; Hunziker 2001) removed it into its own monotypic section and considered it to be unrelated to members of sects. *Pachyphylla* and *Cyphomandropsis*. Members of all three sections were sampled in the current study: *S. betaceum* and *S. diploconos* from sect. *Pachyphylla*, *S. luteoalbum* from sect. *Cyphomandropsis*, and *S. glaucophyllum* from sect. *Glaucophyllum*. These and previous data (Olmstead and Palmer 1992, 1997; Spooner et al. 1993; Bohs 1995; Bohs and Olmstead 1997, 1999) unequivocally identify the well supported (100% BS, 17 DI, 100% PP) Cyphomandra clade within *Solanum* and establish that *S. glaucophyllum* is a member of this clade. They also refute Nee's hypothesis that sects. *Cyphomandropsis* and *Pachyphylla* are closely related to sect. *Pteroidea*, whose sampled species *S. uleanum* here is a member of the Potato clade. However, current sampling is in-sufficient to draw inferences about the monophyly of sections within the Cyphomandra clade.

GEMINATA CLADE. A recent revision of *Solanum* sect. *Geminata* (Knapp 2002) broadly defined the section to include trees and shrubs that are either glabrous or pubescent with simple or dendritic trichomes, and with inflorescences mainly opposite the leaves. The plants are predominantly found in neotropical forests in primary and secondary habitats. With few exceptions, this revision (Knapp 2002) corresponds closely with the strongly supported (100% BS, 26 DI, 100% PP) Geminata clade. Knapp's (2002) definition of sect. *Geminata* included many species traditionally placed in other *Solanum* sections, such as sects. *Holophylla*, *Pseudocapsicum*, and *Indubitaria*, due to perceived differences in hair morphology and inflorescence branching. The molecular data of Bohs (2005) and those presented here show that representatives of sects. *Pseudocapsicum* (*S. pseudocapsicum*) and *Indubitaria* (*S. ochrophyllum*) cluster with members of sect. *Geminata*, supporting Knapp's broad concept of the section. *Solanum delitescens* and *S. havanense*, considered by Knapp (2002) to be of uncertain taxonomic affinities, form a grade on the Geminata clade outside the well-supported group corresponding to sect. *Geminata* sensu Knapp (2002).

The situation with respect to sect. *Holophylla* is more complex. This section is morphologically heterogeneous and has been ill-defined in previous classification schemes. Molecular data confirm that sect. *Holophylla* is not monophyletic. *Solanum argentinum*, included in sect. *Holophylla* in recent taxonomic treatments (Knapp 1989; Nee 1999), is nested within the Geminata clade, but other species considered to belong to sect. *Holophylla* such as *S. crispum*, *S. nitidum*, *S. pubigerum*, and *S. aligerum* emerge in the Dulcamaroid clade. *Solanum inelegans*, postulated by Nee (1999) to belong to sect. *Holophylla*, is a member of the Brevantherum clade.

BREVANTHERUM CLADE. The strongly supported (100% BS, 12 DI, 100% PP), New World Brevantherum clade is divided into two distinct subclades. The first comprises sect. *Gonatotrichum* (*S. adscendens*, *S. turneroides*, and *S. deflexum*) and is sister to a clade that includes sect. *Brevantherum* and its allies, encompassing species in sects. *Brevantherum*, *Extensum*, *Lepidotum*, and *Stellatigeminatum*. In general, species in the latter four sections have stellate trichomes or lepidote scales and oblong anthers with large terminal pores. The distinctions among the four sections are not well-defined morphologically. Child (1998) attempted to delimit the sections largely on the basis of trichome features and branching pattern, but Nee (1999) considered the trichome morphology within this group to be homoplasious and treated sects. *Extensum*, *Lepidotum*, and *Stellatigeminatum* as synonyms of sect. *Brevantherum*. Our data confirm a close relationship among these sections and also resolve *S. inelegans* within this clade.

The species sampled from sect. *Gonatotrichum* (*S. adscendens*, *S. turneroides*, *S. deflexum)*, although belonging to the Brevantherum clade, are morphologically and molecularly very distinct from the rest of the species of the clade. The plants are small annuals or perennials with simple, unbranched, often geniculate hairs. Thus, trichomes in sect. *Gonatotrichum* are strikingly different from the stellate trichomes and lepidote scales observed in its sister group. Trichome morphology is an important character in *Solanum* taxonomy (Seithe 1962, 1979; Roe 1971; Edmonds 1982; Seithe and Anderson 1982), and the trichomes observed in sect. *Gonatotrichum* may arise from a reduction of the stellate trichomes found in other members of the Brevantherum clade. On a larger scale, both simple and branched trichomes are observed within the Geminata clade (discussed above), and stellate hairs are typical, but not ubiquitous, within the Leptostemonum clade. However, relationships among the Brevantherum, Geminata, and Leptostemonum clades are unresolved, and the evolution of branched trichomes among these taxa cannot be inferred from current data.

LEPTOSTEMONUM CLADE. The well-supported Leptostemonum clade (100% BS, 19 DI, 100% PP) includes approximately 450 species of cosmopolitan distribution, with centers of diversity in Central and South America, Australia, and Africa. Members of this clade are referred to as the ''spiny solanums'' because most species possess sharp prickles on the stems and leaves. Additional characteristic morphological features include stellate hairs and tapered anthers with small terminal pores that do not enlarge into longitudinal slits. The morphologically distinct Leptostemonum clade has been recognized at various taxonomic levels since Linnaeus (1753), and was treated most comprehensively by Whalen (1984). Recent DNA sequence data (Levin et al. 2006) confirm the monophyly of *Leptostemonum* sensu stricto (excluding the *S. wendlandii* and *S. nemorense* species groups), results consistent with those observed here. Our data resolve a monophyletic Leptostemonum clade, with *S. accrescens* sister to the other species of the clade. The sister group of the Leptostemonum clade within *Solanum* remains ambiguous, but the *S. wendlandii* and *S. nemorense* groups may be likely candidates (see discussion below).

UNPLACED TAXA. Within *Solanum*, a number of groups are clearly defined morphologically, and the addition of DNA sequence data serves to confirm traditional taxonomic hypotheses (e.g., sect. *Archaesolanum*; Marzell 1927; Danert 1970; D'Arcy 1972, 1991; Symon 1994; Nee 1999; Child and Lester 2001). In other cases, DNA sequence data has provided insight into appropriate taxonomic affinities of some more ambiguously treated groups (e.g., the transfer of *Lycopersicum* and *Cyphomandra* to *Solanum*; Spooner et al. 1993; Bohs 1995). However, some species are notoriously difficult to place using both traditional morphological data and currently available DNA sequence data. This outcome is not surprising; highly divergent taxa that share few obvious morphological synapomorphies with other extant *Solanum* species may also reflect this morphological divergence at the sequence level. A potential for accelerated rates of sequence evolution exists, and inadequate knowledge or availability of closely related species may compound difficulties in inferring the correct phylogenetic placement of these taxa. The taxonomic position of the following species groups remains ambiguous, and further thorough morphological and molecular studies are warranted.

Whalen (1984) included *S. nemorense* and *S. hoehnei* in the *S. nemorense* species group within subgenus *Leptostemonum* based on the presence of prickles and attenuate anthers. Although the group lacks the stellate hairs characteristic of subgenus *Leptostemonum*, Whalen (1984) rejected other *Solanum* subgenera as more appropriate locations for this group. He suggested a close relationship between the *S. nemorense* group and the *S. wendlandii* group, which also has prickles and lacks stellate hairs, but recognized that both groups were phylogenetically isolated within *Solanum*. An additional species, *S. reptans* Bunbury, treated by Whalen (1984) in the *S. nemorense* group, was sampled in Levin et al. (2006) and was resolved as part of the *S. nemorense*/*S. hoehnei* clade in their analyses. Our data confirm a close relationship between *S. nemorense* and *S. hoehnei* (95% BS, 5 DI, 100% PP), and also suggest that the *S. nemorense*/*S. hoehnei* clade is somewhat isolated within *Solanum*; it is placed sister to the larger Leptostemonum + Brevantherum + Geminata clade, but the relationship between the *S. nemorense*/*S. hoehnei* clade and the other three clades is unclear.

Our data identify *S. wendlandii* and *S. allophyllum* as sister species, but with poor support (52% BS, 1 DI, 84% PP). Whalen (1984) treated the *S. wendlandii* species group within subgenus *Leptostemonum* based on the presence of small, recurved prickles and weakly attenuate anthers, although the six species in the group lack stellate hairs. Levin et al (2006) also sampled *S. bicorne* Dunal (determined as *S. refractum* Hook. in Levin et al. 2006), one of the five additional species Whalen (1984) allied with *S. wendlandii*. *Solanum bicorne* was resolved as sister to *S. wendlandii* (Levin et al. 2006), but the position of the *S. wendlandii* group with respect to the Leptostemonum clade was unresolved.

The taxonomic position of *S. allophyllum* is puzzling; the phylogeny suggests an affiliation with *S. wendlandii*, although this relationship is poorly supported and may be an artifact of sparse taxon sampling. Child (1984b) considered *S. allophyllum* to belong to the genus *Cyphomandra* and erected *Cyphomandra* sect. *Allophylla* to house *S. allophyllum* and *S. mapiriense*. Bohs (1990) later transferred sect. *Allophylla* from *Cyphomandra* to *Solanum* and described another species of the section, *S. morellifolium* Bohs. Although Bohs (1990) identified numerous morphological similarities supporting a close relationship among *S. allophyllum*, *S. mapiriense*, and *S. morellifolium*, she was unable to place these taxa with certainty into any existing *Solanum* subgenus. In the molecular trees, *S. allophyllum* and *S. mapiriense*, the only sampled members of sect. *Allophylla*, did not emerge as sister taxa. Instead, *S. mapiriense* is sister to *S. clandestinum* (99% BS, 8 DI) and *S. allophyllum* is sister to *S. wendlandii* (52% BS, 1 DI, 84% PP). The monophyly of sect. *Allophylla* and the relationships of *S. allophyllum* are still unclear and await further sampling and molecular data.

Solanum clandestinum is a newly described species (Nee et al. 2006) whose phylogenetic placement also is equivocal. The *ndhF* data alone place it in a clade with *S. wendlandii*, *S. allophyllum*, and *S. mapiriense*, but with poor support (58% BS, 1 DI). Its position is unresolved within *Solanum* in the *trnT-F* analysis, but *waxy* places it sister to *S. mapiriense* (99% BS, 8 DI), similar to the results of the combined analysis. *Solanum clandestinum* and *S. mapiriense* are both endemic to the Yungas of La Paz in northwestern Bolivia, but they are divergent morphologically. For instance, *S. clandestinum* has relatively broad, blunt anthers with pores opening into longitudinal slits, whereas those of *S. mapiriense* are strongly tapered and dehisce by small terminal pores.

Further analyses of additional DNA sequences with thorough taxonomic sampling will be necessary to elucidate the phylogenetic position of *S. wendlandii*, *S. allophyllum*, *S. mapiriense*, and *S. clandestinum*. These species appear to represent divergent and isolated lineages within *Solanum* and adequate taxon sampling is crucial to eliminate the spurious results of long-branch attraction (Felsenstein 1978; Hendy and Penny 1989; Hillis 1996, 1998; Graybeal 1998; Bergsten 2005). Because these species are morphologically distinctive within *Solanum*, their phylogenetic position will be essential to interpret larger patterns of character evolution within the genus. For example, like *S. nemorense and S. hoehnei*, the *S. wendlandii* species group possesses prickles and weakly attenuate anthers, but lacks stellate hairs. Depending on the resolution of clades in this part of the *Solanum* phylogeny, inferences may be made about the evolution of prickles and their homology in various *Solanum* groups. Should the *S. nemorense* and *S. wendlandii* species groups emerge as sister to the Leptostemonum clade, prickles may be inferred to have evolved once and may be homologous structures in *Solanum*. However, as these results and those of Levin et al. (2006) imply, the *S. nemorense* and/or *S. wendlandii* groups may not be sister to the Leptostemonum clade, and prickles may be derived independently in multiple *Solanum* lineages. This could provide an opportunity to investigate basic questions of homology and whether these apparently homologous structures share a similar genetic and developmental basis.

These analyses of relationships among the major *Solanum* clades provide the best resolved phylogeny available for the genus to date. In addition to confirming the taxonomic composition of previously identified clades (Bohs 2005), the deeper level relationships among those clades are becoming apparent. This phylogeny will function as a working hypothesis for future systematic and evolutionary studies within *Solanum* and should be particularly helpful in choosing appropriate outgroups for fine-scale analyses within the major *Solanum* clades. However, our understanding of evolution within *Solanum* is far from complete. The sister group to the Leptostemonum clade is unclear, as are relationships among the groups within the Dulcamaroid clade. The relationships and appropriate taxonomic treatment of *S. nemorense*, *S. hoehnei*, *S. wendlandii*, *S. allophyllum*, *S. mapiriense*, and *S. clandestinum* and their closest relatives remain largely unknown, and will require considerable work using morphological and DNA sequence markers. We recommend that formal nomenclatural changes be postponed until well-supported, stable topologies are attained at all taxonomic levels in the *Solanum* phylogeny.

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Appendix 1. Summary of species, collection location, vouchers, and GenBank accession numbers for taxa used in this study provided in the order *ndhF*, *trnT-F*, and *waxy*. BIRM – cultivated at the University of Birmingham, U.K. NIJ – cultivated at Radboud University, Nijmegen, The Netherlands. PI – U.S.D.A. Plant Introduction number. D'Arcy collection – cultivated at MO.

S. abutiloides (Griseb.) Bitter & Lillo – BIRM S.0655, *Olmstead S-73* (WTU); U47415, AY266236, AY562948. ***S. accrescens*** Standl. & C. V. Morton – Costa Rica, *Bohs 2556* (UT); AF500795, DQ180473, AY996375. ***S. adhaerens*** Roem. & Schult. – Costa Rica, *Bohs 2473* (UT); AF224061, DQ180474, AY996377. ***S. adscendens*** Sendtn. – Bolivia, *Bohs & Nee 2738* (UT); AF500796, DQ180421, DQ169013. ***S. aethiopicum*** L. – BIRM S.0344, *Olmstead S-74* (WTU); AF500797, DQ180394, AY996378. ***S. aggregatum*** Jacq. – South Africa, *Olmstead 99-25* (WTU); AF500798, DQ180460, DQ169014. ***S. aligerum*** Schltdl. – Bolivia, *Nee et al. 51822* (NY); AF500799, DQ180441, DQ169015. ***S. allophyllum*** (Miers) Standl. – Panama, *Bohs 2339* (UT); U47416, DQ180422, AY996379. ***S. amygdalifolium*** Steud. – Argentina, *Nee & Bohs 50840* (NY); AF500800, DQ180442, DQ169016. ***S. aphyodendron*** S. Knapp – Colombia, *Olmstead S-92* (WTU); AF500801, DQ180423, DQ169017. ***S. appendiculatum*** Dunal – Mexico, *Anderson 1401* (CONN); AF224062, DQ180461, DQ169018. ***S. arboreum*** Dunal – Costa Rica, *Bohs 2521* (UT); U47417, DQ180424, AY996381. ***S. argentinum*** Bitter & Lillo – Argentina, *Bohs 2539* (UT); U72752, DQ180425, AY996382. ***S. aviculare*** G. Forst. – BIRM S.0809, no voucher; U47418, AY562952, AY559238. ***S. betaceum*** Cav. – Bolivia, *Bohs 2468* (UT); U47428, DQ180426, AY996387. ***S. brevicaule*** Bitter – Bolivia, *Hawkes et al. 6701* (PTIS); AF500803, DQ180443, DQ169019. ***S. bulbocastanum*** Dunal – Mexico, *Tarn 153* (PTIS); AF500804, DQ180444, DQ169020. ***S. caesium*** Griseb. – Bolivia, *Bohs et al. 2815* (UT); AF500805, DQ180445, DQ169021. ***S. calileguae*** Cabrera – Argentina, *Nee & Bohs 50809* (NY); AF500806, EF068252, DQ169022. ***S. campanulatum*** R. Br. – BIRM S.0387, *Olmstead S-78* (WTU); AF500807, DQ180395, AY996388. ***S. campechiense*** L. – Costa Rica, *Bohs 2536* (UT); AF224071, DQ180475, AY996389. ***S. candidum*** Lindl. – *ndhF*: BIRM S.0975, *Olmstead S-100* (WTU), *trnT-F*, *waxy*: Costa Rica, *Bohs 2898* (UT); AF224072, AY266237, AY562953. ***S. capsicoides*** All. – Peru, *Bohs 2451* (UT); AF500808, AY266251, AY562954. ***S. carolinense*** L. – BIRM S.1816, *Olmstead S-77* (WTU); AF500811, DQ180476, AY996392. ***S. chenopodinum*** F. Muell. – BIRM S.0813, no voucher; AF500812, DQ180396, AY996393. **S.**

cinereum R. Br. – NIJ 904750120, *Bohs 2852* (UT); AF500813, DQ180397, AY996394. ***S. citrullifolium*** A. Braun – BIRM S.0127, *Olmstead S-79* (WTU); AF500814, DQ180477, AY996395. ***S. clandestinum*** Bohs – Bolivia, *Nee et al. 51781* (NY); DQ392957, DQ180462, DQ169023. ***S. cleistogamum*** Symon – BIRM S.0844, *Olmstead S-80* (WTU); AF500815, DQ180478, AY996397. ***S. conditum*** C. V. Morton – Bolivia, *Bohs & Nee 2733* (NY); AF500816, DQ180479, AY996400. ***S. cordovense*** Sessé & Moç. – Costa Rica, *Bohs 2693* (UT); U72751, DQ180480, AY996401. ***S. crinitipes*** Dunal – Colombia, *Olmstead S-81* (WTU); AF500817, DQ180481, AY996402. ***S. crinitum*** Lam. – NIJ 924750049, *Bohs 2850* (UT); AF500818, DQ180482, AY996403. ***S. crispum*** Ruiz & Pav. – BIRM S.0486, no voucher; AF500819, DQ180446, DQ169024. ***S. deflexum*** Greenm. – Costa Rica, *Bohs 2715* (UT); AF500820, DQ180427, DQ169025. ***S. delitescens*** C. V. Morton – Argentina, *Nee & Bohs 50810* (NY); AF500821, DQ180428, DQ169026. ***S. diploconos*** (Mart.) Bohs – Brazil, *Bohs 2335* (UT); AY049014, DQ180429, AY996407. ***S. drymophilum*** O. E. Schulz – Puerto Rico, *Bohs 2461* (UT); AF500823, DQ180483, AY996409. ***S. dulcamara*** L. – USA, no voucher; U47419, AY266231, AY996410. ***S. echinatum*** R. Br. – *ndhF*, *trnT-F*: NIJ 954750052, *Bohs 2727* (UT), *waxy*: Australia, *Symon 17102* (AD); AF500824, DQ180398, AY996411. ***S. elaeagnifolium*** Cav. – *ndhF*: USA, *Olmstead S-82* (WTU), *trnT-F*: Paraguay, *Bohs 3204* (UT), *waxy*: Paraguay, *Bohs 3199* (UT); AF224067, DQ180399, AY996412. ***S. etuberosum*** Lindl. – Chile, PI 498311, *Contreras 1322* (UAC); AF500825, DQ180463, DQ169027. ***S. evolvulifolium*** Greenm. – Panama, *Knapp & Mallet 9178* (BM); AF500826, DQ180464, DQ169028. ***S. ferocissimum*** Lindl. – BIRM S.0819, *Olmstead S-83* (WTU); AF500827, DQ180400, AY996415. ***S. fiebrigii*** Bitter – Bolivia, *Bohs et al. 2784* (UT); AF500828, DQ180447, DQ169029. ***S. fraxinifolium*** Dunal – Costa Rica, *Bohs 2558* (UT); AF500810, DQ180465, AY996416. ***S. furfuraceum*** R. Br. – BIRM S.1442, *Olmstead S-84* (WTU); AF500829, DQ180401, AY996417. ***S. glaucophyllum*** Desf. – D'Arcy collection, no voucher; U72753, DQ180430, AY996418. ***S. havanense*** Jacq. – NIJ 904750122, *Bohs 3076* (UT); AF500830, DQ180431, DQ169030. ***S. herculeum*** Bohs – Morocco, *Jury 13742* (RNG); AF224065, DQ180466, DQ169031. ***S. hindsianum*** Benth. – Mexico, *Bohs 2975* (UT); AF500831, DQ180402, AY996424. ***S. hoehnei*** C. V. Morton – Brazil, *Folli 1668* (MO); AF500832, DQ180484, AY996426. ***S. inelegans*** Rusby – Bolivia, *Nee et al. 51813* (NY); AF500833, DQ180432, DQ169032. ***S. ipomoeoides*** Chodat & Hassl. – Bolivia, *Bohs & Nee 2766* (UT); AF500834, DQ180448, DQ169033. ***S. jamaicense*** Mill. – BIRM S.1209, *Olmstead S-85* (WTU); AF224073, DQ180485, AY562956. ***S. juglandifolium*** Dunal – Colombia, *Rick et al. 7546* (PTIS); AF500837, DQ180449, DQ169034. ***S. laciniatum*** Aiton – New Zealand, *Bohs 2528* (UT); U47420, DQ180467, AY996431. ***S. lepidotum*** Dunal – Costa Rica, *Bohs 2621* (UT); AF500838, DQ180486, DQ169035. ***S. lidii*** Sunding – NIJ 934750022, *Bohs 2903* (UT); AF500839, DQ180403, AY996434. ***S. luteoalbum*** Pers. – BIRM S.0042, *Bohs 2337* (UT); U72749, DQ180433, AY562957. ***S. lycopersicum*** L. – USA (cultivated), no voucher; U08921, DQ180450, DQ169036. ***S. macrocarpon*** L. – BIRM S.0133, *Olmstead S-88* (WTU); AF224068, DQ180404, AY996436. ***S. mahoriensis*** D'Arcy & Rakot. – Madagascar, *Bohs 2576* (UT); AF500841, DQ180405, AY996437. ***S. mammosum*** L. – BIRM S.0983, *Olmstead S-89* (WTU); AF224074, AY266232, AY562958. ***S. mapiriense*** Bitter – Bolivia, *Nee & Solomon 30305* (UT); AF500842, DQ180434, AY996439. ***S. mauritianum*** Scop. – BIRM S.0860, *Olmstead S-90* (WTU); AF500843, DQ180487, DQ169037. ***S. melongena*** L. – BIRM S.0657, *Olmstead S-91* (WTU); AF224069, DQ180406, AY562959. ***S. montanum*** L. –NIJ 904750205, *Bohs 2870* (UT); AF500844, DQ180468, AY996443. ***S. muricatum*** Aiton – Colombia, *Olmstead S-93* (WTU); AF500846, DQ180469, DQ169038. ***S. nemorense*** Dunal – Bolivia, *Bohs & Nee 2757* (UT); AF500847, DQ180488, AY996447. ***S. nitidum*** Ruiz & Pav. – Bolivia, *Nee 31944* (NY); AF224075, DQ180451, DQ169039. ***S. ochrophyllum*** Van Heurck & Müll. Arg. – Bolivia, *Bohs & Nee 2805* (UT); AF500848, DQ180435, DQ169040. ***S. palitans*** C. V. Morton – BIRM S.0837/70, *Bohs 2449* (UT); AF224064, DQ180452, AY996449. ***S. physalifolium*** Rusby var. ***nitidibaccatum*** (Bitter) Edmonds – USA, *Bohs 2467* (UT); U47421, EF068253, DQ169041. ***S. pinnatisectum*** Dunal – Mexico, *Tarn 205A* (PTIS); AF500850, DQ180453, DQ169042. ***S. prinophyllum*** Dunal – NIJ 904750171, *Bohs 2725* (UT); AF500852, DQ180407, AY996456. ***S. pseudocapsicum*** L. – BIRM S.0870, no voucher; U47422, DQ180436, AY562963. ***S. ptychanthum*** Dunal – USA, *Olmstead S-94* (WTU); U47423, DQ180454, AY996457. ***S. pubigerum*** Dunal – NIJ 904750104, no voucher; AF500853, DQ180455, DQ169043. ***S. pyracanthos*** Lam. – USA (cultivated), *Olmstead S-95* (WTU); AF500854, DQ180408, AY996459. ***S. riojense*** Bitter – Argentina, *Nee & Bohs 50843* (NY); AF500856, DQ180456, DQ169044. ***S. rostratum*** Dunal – USA, no voucher; U47424, DQ180489, AY996463. ***S. rovirosanum*** Donn. Sm. – Costa Rica, *Bohs 2919* (UT); AF500857, DQ180437, DQ169045. ***S. rugosum*** Dunal – Costa Rica, *Bohs 3011* (UT); AF500858, DQ180490, DQ169046. ***S. sandwicense*** Hook. & Arn. – Hawaii, *Bohs 2992* (UT); AF500859, DQ180409, AY996464. ***S. schimperianum*** Hochst. – BIRM S.1538, *Olmstead S-97* (WTU); AF500860, DQ180410, AY996465. ***S. schlechtendalianum*** Walp. – Costa Rica, *Bohs 2915* (UT); AF500861, DQ180491, DQ169047. ***S. seaforthianum*** Andrews – BIRM S.0051, no voucher; U47425, DQ180438, DQ169048. ***S. sisymbriifolium*** Lam. – Argentina, *Bohs 2533* (UT); AF500862, AY266235, AY562967. ***S. stramonifolium*** Jacq. – Peru, *Whalen 860* (HUT); AF500863, AY266263, AY562970. ***S. thelopodium*** Sendtn. – Bolivia, *Nee & Bohs 50858* (NY); AF500865, DQ180470, AY996471. ***S. toliaraea*** D'Arcy & Rakot. – Madagascar, *Bohs 2574* (UT); AF500866, DQ180411, AY996472. ***S. torvum*** Sw. – BIRM S.0839, *Olmstead S-101* (WTU); L76286, AY266246, AY562972. ***S. tridynamum*** Dunal – BIRM S.1831, *Olmstead S-102* (WTU); AF500867, DQ180412, AY996474. ***S. triflorum*** Nutt. – USA, *Bohs 3062* (UT); AF500868, DQ180457, DQ169049. ***S. tripartitum*** Dunal – BIRM S.0708/71, *Bohs 2465* (UT); U72750, DQ180458, DQ169050. ***S. trisectum*** Dunal – France, *Bohs 2718* (UT); AF224063, DQ180471, AY996475. ***S. turneroides*** Chodat – Bolivia, *Nee et al. 51716* (NY); AF500869, DQ180439, DQ169051. ***S. uleanum*** Bitter – D'Arcy collection, *Bohs 2720* (UT); AF500870, DQ180472, DQ169052. ***S. vespertilio*** Aiton – BIRM S.2091, *Olmstead S-103* (WTU); AF224070, DQ180413, AY996476. ***S. villosum*** Mill. – Iran, *Bohs 2553* (UT); AF224066, DQ180459, DQ169053. ***S. wendlandii*** Hook. f. – BIRM S.0488, no voucher; U47427, DQ180440, AY562974. Outgroups: ***Capsicum baccatum*** L. var. ***pendulum*** (Willd.) Eshbaugh – *ndhF*: Bolivia, *Eshbaugh 1584* (MU), *trnT-F*, *waxy*: USA (cultivated), *Bohs 2564* (UT); U08916, DQ180415, DQ169007. ***Capsicum chacoense*** Hunz. – Bolivia, *Eshbaugh 1586A* (MU); AF500809, DQ180416, DQ169008. ***Jaltomata procumbens*** (Cav.) J. L. Gentry – Mexico, *Davis 1189A*; U47429, DQ180419, AY996374. ***Jaltomata sinuosa*** (Miers) Mione – Bolivia, *Nee et al. 51830* (NY); AF500835, DQ180418, DQ169009. ***Lycianthes heteroclita*** (Sendtn.) Bitter – Costa Rica, *Bohs 2376* (UT); U72756, DQ180414, DQ169010. ***Lycianthes rantonnei*** (Carrière) Bitter – BIRM S.0928, *Olmstead S-96* (WTU); AF500840, DQ180417, DQ169011. ***Physalis alkekengi*** L. – D'Arcy collection, *D'Arcy 17707* (MO); U08927, DQ180420, DQ169012.