MAJOR CLADES IN SOLANUM BASED ON ndhF SEQUENCE DATA

Lynn Bohs

ABSTRACT. Analysis of sequence data from the chloroplast gene ndhF 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: ndhF, 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
   ca. 70 species, New World
   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 ndhF. 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 ndhF 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.


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extracted with the modified CTAB method were purified using cesium chloride density gradient centrifugation or a phenol-chloroform protocol. Amplification and sequencing of the *ndhF* 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 *ndhF* 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 *ndhF* 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. piuare* versus *S. doddsii*. *Solanum schlechtendalianum* and *S. lepidotum* had identical *ndhF* 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 *Lycopersicon*, *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, Archaeosolanum, 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 *ndhF* data:

1. **Thelopodium clade**
   - ca. 3 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 *ndhF* 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 ndhF 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. pycthanthum*, *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 ndhF 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]*

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 ndhF 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

c. 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 *ndhF* 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

c. 200–300 spp., New World

Included taxa:

- *Solanum* subg. *Potatoe* (G. Don) D’Arcy
  - *Solanum* sect. *Anarrhichomenum* Bitter*
  - *Solanum* sect. *Basarthrum*

- *Solanum* sect. *Neolycopersicon* Correll
- *Solanum* sect. *Juglandifolium* (Ryd.) A. Child*
- *Solanum* sect. *Etuberoseum* (Bukasov & Kamaraz) A. Child*
- *Solanum* sect. *Articulatum* (Correll) A. Child
- *Solanum* sect. *Taeniotrichum* A. Child
- *Solanum* subg. *Bassovia* (Aubl.)
  - *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. evolvolifolium* as members of the section. These species are sampled in the *ndhF* 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 *ndhF* data indicate that section Pteroidea belongs to the Potato clade, and that the sampled representatives of the subgenera Potatooe 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 Potatooe. Whether members of the subgenus Bassovia possess these types of alkaloids is unknown.

Child (1990) placed *Solanum evolvolifolium* in section Anarrhichomenum, whereas Nee (1999) placed this species in section Herpystichum. The *ndhF* data show that *S. evolvolifolium* 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 Potatooe, 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 *ndhF* 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. *Campanulisisolanum* 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 *ndhF* 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 *ndhF* 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 *ndhF* 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 *ndhF* 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 ndhF 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 ndhF 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.

Solanum 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 ndhF 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 ndhF 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 ndhF
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 *ndhF* 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. *Herposolanum* (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 *ndhF* (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 *ndhF* and nuclear ITS sequence data is under way (L. Bohs, unpublished data) and will be summarized in a later publication.

The *ndhF* 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 *ndhF* 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 *ndhF* 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 *ndhF* 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 non-molecular synapomorphies that support the *ndhF* 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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**Literature Cited**

MAJOR CLADES IN SOLANUM BASED ON ndhF SEQUENCE DATA


Figure 1. Strict consensus of 18,200 trees of 1053 steps from parsimony analysis of *ndhF* data. Numbers above branches are bootstrap values (500 replicates). Major clades in *Solanum* discussed in the text are labeled.
MAJOR CLADES IN SOLANUM BASED ON ndhF SEQUENCE DATA

Figure 1 continued.

Dulcamaroid

Morelloid

Potato

African non-spiny

Normania

Archaesolanum

Regmandra

Thelopodium

Solanum wallacei
Solanum seaforthianum
Solanum dulcamara
Solanum aligerum
Solanum nitidum
Solanum crispum
Solanum amygdalifolium
Solanum jasminoides
Solanum calliaguae
Solanum pubigerum
Solanum ipomeoides
Solanum ptychanthum
Solanum villosum
Solanum fiebrigii
Solanum triflorum
Solanum riojense
Solanum physalifolium
Solanum caesium
Solanum tripartitum
Solanum palitans
Solanum stenophyllidium
Solanum tuberosum
Solanum brevicaule
Solanum bulbocastanum
Solanum doddsii
Solanum pinnatisectum
Solanum piurae
Solanum lycopersicum
Solanum juglandifolium
Solanum etuberosum
Solanum fraxinifolium
Solanum muralatum
Solanum appendiculatum
Solanum uleanum
Solanum trizygum
Solanum phaseoloides
Solanum evolvulifolium
Solanum aggregatum
Solanum terminale
Solanum quadrangularare
Solanum trisectum
Solanum herculcum
Solanum aviculare
Solanum lacinatum
Solanum montanum
Solanum multifidum
Solanum thelopodium
Capsicum baccatum
Capsicum chacoense
Lycianthes rantonnei
Lycianthes heteroclena
Jaltomata sinuosa
Jaltomata procumbens
Witheringia solanaceae
Physalis alkekengi