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PHYLOGENETIC RELATIONSHIPS AMONG THE "SPINY SOLANUMS" (*SOLANUM* SUBGENUS *LEPTOSTEMONUM*, SOLANACEAE)[1]

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Species of *Solanum* subgenus *Leptostemonum* comprise almost one third of the genus and are distributed worldwide. Members of this group are defined by their sharp epidermal prickles; thus, they are commonly referred to as the "spiny solanums." This subgenus includes a number of economically important species such as the Old World eggplants, as well as locally cultivated New World species such as the naranjilla and cocona. Given the size and importance of this group we have examined phylogenetic relationships across subgenus *Leptostemonum*, including a large sampling of species from previously defined species groups within the subgenus. Evolutionary relationships were inferred using DNA sequence data from two nuclear regions (ITS and the granule-bound starch synthase gene [GBSSI or *waxy*]) and one chloroplast spacer region (*trnS-trnG*). Results suggest that *Solanum* subgenus *Leptostemonum* is monophyletic when the *S. wendlandii* and *S. nemorense* species groups are excluded. We have defined 10 clades within subgenus *Leptostemonum*, some of which correspond to previously circumscribed species groups or sections. Most of the Old World species of subgenus *Leptostemonum* belong to a single species-rich clade. Sharp prickles and/or stellate hairs evolved more than once in *Solanum*, and floral heterandry originated multiple times within the "spiny solanums."

Key words: granule-bound starch synthase gene (GBSSI); heterandry; ITS; *Leptostemonum*; Solanaceae; *Solanum*; *trnS-trnG*; *waxy*.

Solanum subgenus *Leptostemonum* (Dunal) Bitter are a large group (ca. 350–450 species) within *Solanum*, comprising almost one third of the genus. Species of subgenus *Leptostemonum* have a worldwide distribution, with the highest species richness in Central and South America, Africa, and Australia. This group has been recognized since at least the time of Linnaeus (1753), with rank and circumscription varying with the taxonomic treatment. One of the main characteristics defining this subgenus is the presence of sharp epidermal prickles on stems and leaves in all but a few taxa; thus, species of subgenus *Leptostemonum* are commonly known as the "spiny solanums." Most members of this group also have stellate hairs and long, attenuate anthers with small terminal pores; the name *Leptostemonum* is due to these distinct anthers. The economically important eggplants *S. melongena* (aubergine or brinjal eggplant), *S. aethiopicum* (scarlet eggplant), and *S. macrocarpon* (*gboma* eggplant), as well as the cultivated *S. quitoense* (naranjilla or lulo) and *S. sessiliflorum* (cocona) belong to this subgenus.

Regional treatments of *Solanum* have been provided by Symon (1981), Jaeger (1985), and Nee (1999), among others; however, the most comprehensive treatment of the "spiny solanums" is that of Whalen (1984). Based on morphology and biogeography, Whalen (1984) recognized 33 informal species groups within subgenus *Leptostemonum* as well as 36 unplaced *Solanum* species. Whalen (1984) summarized the diagnostic characters, geographical distributions, and component species of each of the 33 species groups and placed them in a hypothetical phylogenetic scheme based on morphological characters, such that his work serves as an invaluable guide to relationships among this large, diverse subgenus. Although Whalen's treatment is arguably the most useful, Whalen (1984) was not the first to recognize taxonomic groups of species within subgenus *Leptostemonum*; the previously described sections of subgenus *Leptostemonum* as they relate to Whalen's species groups are shown in Table 1.

Molecular phylogenetic studies of the genus *Solanum* based on chloroplast DNA restriction sites (Olmstead and Palmer, 1997) support the monophyly of subgenus *Leptostemonum* sensu Whalen (1984). However, more recent studies using chloroplast and nuclear DNA sequence data and greater taxon sampling (Bohs and Olmstead, 1997, 1999, 2001; Bohs, 2005) suggest that the *S. wendlandii* group and perhaps also the *S. nemorense* group, both of which have prickles but lack stellate hairs, may not belong within the subgenus.

Thus, the major goals of this study are to (1) test the monophyly of subgenus *Leptostemonum* sensu Whalen (1984) and determine the closest relatives of the subgenus, (2) examine relationships within subgenus *Leptostemonum* and evaluate the validity of species groups as circumscribed by Whalen (1984), and (3) examine floral evolution in subgenus *Leptostemonum* in light of phylogenetic relationships. To accomplish these goals, we used DNA sequence data from two nuclear gene regions, the internal transcribed spacer (ITS) region of nuclear ribosomal DNA and the granule-bound starch synthase gene (*waxy* or GBSSI), and one chloroplast spacer region (*trnS-trnG*).

MATERIALS AND METHODS

Taxon sampling—This study included a broad sampling across the various species groups as circumscribed by Whalen (1984) within subgenus *Leptostemonum* (Table 1). Of the 33 named species groups of Whalen (1984), species were sampled from all but six of the groups (the unsampled groups together comprise ca. 24 species [ca. 5–7% of the species in the subgenus]). Thirty-six additional taxa were unplaced by Whalen (1984), and we were able

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TABLE 1. The species groups of Whalen (1984) described for subgenus *Leptostemonum*. The previously described sections for each species group are indicated (where applicable). When multiple named sections exist for a given species group, the sectional name given in D'Arcy (1991) is listed. Also shown is each species group's approximate size and geographic distribution as given by Whalen (1984). Asterisks indicate those species groups included in the present study.

Species group	Section	Species no. and range
*Solanum anguivi**	*Oliganthes* (Dunal) Bitter	40 Africa, Asia
*Solanum arundo**	*Ischyracanthum* Bitter	3 Africa
Solanum asterophorum	N/A	2–3 Brazil
*Solanum bahamense**	*Persicariae* Dunal	5 Florida, Caribbean Islands
*Solanum bumeliifolium**	*Croatianum* D'Arcy & Keating	3 Madagascar
*Solanum crinitum**	*Crinitum* (Whalen) Child	8 S. America
*Solanum crotonoides**	N/A	4 Greater Antilles
*Solanum dioicum**	N/A	16 Australia
*Solanum dunalianum**	*Dunaliana* Bitter (grad. ambig.)	20 S. Pacific, northern Australia
*Solanum ellipticum**	*Leprophora* Dunal	35 Australia; 1 America
*Solanum erythrotrichum**	*Erythrotrichum* (Whalen) Child	25 Central to S. America
*Solanum ferocissimum**	N/A	10 Australia
*Solanum giganteum**	*Torvaria* (Dunal) Bitter	10 Africa
*Solanum hystrix**	N/A	8 Australia
*Solanum incanum**	*Melongena* (Mill.) Dunal	12 Africa, Asia
Solanum jubae	*Somalanum* Bitter	5 Somalia, Ethiopia, Kenya
*Solanum lanceifolium**	*Micracantha* Dunal	15 Mexico to S. America
*Solanum macoorai**	N/A	8 Australia; 1 Philippines
*Solanum mammosum**	*Acanthophora* Dunal	20 Mexico to S. America
*Solanum multispinum**	N/A	7 S. America
*Solanum nemorense**	*Nemorense* Child	6 Amazon Basin, SE Brazil
*Solanum polytrichum**	*Polytrichum* (Whalen) Child	8 S. America
*Solanum quitoense**	*Lasiocarpa* (Dunal) D'Arcy	12 Mexico to S. America, Asia, Polynesia
*Solanum rostratum**	*Androceras* (Nutt.) Marzell	12 SW US, Mexico
*Solanum sandwicense**	*Irenosolanum* Bitter	3 Hawaiian Islands
Solanum subinerme	*Subinermia* Dunal	3 northern S. America
*Solanum thruppii**	*Monodolichopus* Bitter	2 E. Africa
*Solanum torvum**	*Torva* Nees	50 Mexico to S. America
*Solanum vespertilio**	*Nycterium* (Vent.) Walp.	4 Mexico, Canary Islands
Solanum wacketii	N/A	4 Brazil
*Solanum wendlandii**	*Aculeigerum* Seithe	6 Mexico to S. America
Solanum yucatanum	N/A	4 southern Mexico to northern S. America
Unnamed	N/A	5 Colombian Andes, Amazon Basin

Note: N/A = no published sectional name available.

to include 11 of these taxa in the present study. One Australian *Solanum* species included in the analysis is currently being described (Brennan et al., in press); it is referred to as "*Solanum* sp. nov." in this paper. In addition to the 112 taxa sampled from subgenus *Leptostemonum*, 21 *Solanum* species from outside this subgenus were included, as well as *Jaltomata procumbens*, which has previously been found to be sister to *Solanum* (Bohs, 2005). All 134 taxa with voucher information and GenBank accession numbers are listed in the Appendix.

DNA extraction, amplification, and sequencing—Total genomic DNA was extracted from fresh, silica-gel-dried, or herbarium material using the protocols described in Bohs and Olmstead (1997, 2001) and Bohs (2005).

ITS—Amplification of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA, composed of ITS1, the 5.8S gene, and ITS2 (Baldwin, 1992; Baldwin et al., 1995) was done using primers ITSleu1 (5′-GTC CAC TGA ACC TTA TCA TTT AG-3′; Bohs and Olmstead, 2001) and ITS4 (5′-TCC TCC GCT TAT TGA TAT GC-3′; White et al., 1990). PCR conditions were as in Bohs and Olmstead (2001), and PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Valencia, California, USA). Sequencing was done in both directions on an ABI automated sequencer (Applied Biosystems, Foster City, California, USA) by the University of Utah DNA Sequencing Core Facility using ITS4 and ITS5HP (5′-GGA AGG AGA AGT CGT AAC AAG G-3′; Hershkovitz and Zimmer, 1996). For a few taxa, sequencing was also done with one or two internal ITS primers (White et al., 1990).

Waxy—For some species, amplification of the 3′ end of exon 1 through the 3′ end of exon 10 of the nuclear GBSSI gene was done using primers 5′old (5′-GGG TAC TGA GGT TGG TCC TT-3′; D. M. Spooner, USDA, University of Wisconsin, Madison, Wisconsin, USA) and 2R (5′-GTT CCA TAT CGC ATA GCA TG-3′; Miller et al., 1999, but note that one base is missing in the primer sequence given in this reference). Alternatively, amplification of the 5′ end of exon 2 through the 3′ end of exon 10 was done using primer waxyF (5′-CGG GTA ATG ACA ATA TCC CC-3′), a *Solanum*-specific version of primer 181F (Walsh and Hoot, 2001), in combination with the 2R reverse primer (see Fig. 2 in Levin et al., 2005); some amplifications were done with forward primer 181F (5′-CGG GTA ATG ACA ATA TST CC-3′; Walsh and Hoot, 2001).

For two recalcitrant DNAs, *waxy* was amplified in two separate pieces using the primer pair waxyF and 1171R (5′-TCA TAC CCA TCA ATG AAA TC-3′; Walsh and Hoot, 2001) and the primer pair 1058F (5′-ATT CCC TGC TAC TTG AAG TC-3′; a forward primer located in exon 6) and 2R. Reaction mixtures of 25 μL contained 2.5 μL of 10× Mg-free buffer, 2.5 mM $MgCl_2$, 0.25 mM dNTPs, 0.08 μM of each primer, 0.625 units of *Taq* polymerase, and 1 μL DNA. For 5′old and 2R and 181F and 2R, thermal cycler conditions are as in Levin et al. (2005). When using waxyF and 2R, a touchdown procedure was used with an initial denaturing at 94°C for 4 min; 10 cycles at 94°C for 30 s, 55°–51°C (decreasing one degree every two cycles) for 1 min, 72°C for 2 min; 30 cycles at 94°C for 30 s, 50°C for 1 min, 72°C for 2 min; ending with an extension at 72°C for 10 min. The thermal cycler program used with waxyF and 1171R was also a touchdown: an initial denaturing at 94°C for 4 min; 10 cycles at 94°C for 30 s, 50°–46°C (decreasing one degree

TABLE 2. Comparison of the data sets for the two nuclear gene regions and one chloroplast intergenic region. Note that the ITS and *trnS-trnG* data include 134 taxa and the *waxy* data include 131 taxa.

Statistic	ITS	*waxy*	*trnS-trnG*
Range of raw length	580–655 bp	1719–1872 bp	648–713 bp
Aligned length	737 bp	1947 bp	1004 bp
Variable sites (proportion)	357 (0.48)	890 (0.46)	267 (0.27)
PI sites (proportion)	254 (0.34)	521 (0.27)	129 (0.13)
Range of pairwise distances	0–0.150	0–0.080	0–0.048
CI (RC); RI	0.30 (0.19); 0.61	0.67 (0.57); 0.85	0.67 (0.55); 0.82

Note: Parsimony-informative = PI; consistency index = CI (RC = rescaled CI); retention index = RI.

every two cycles) for 1 min, 72°C for 1 min; 30 cycles at 94°C for 30 s, 45°C for 1 min, 72°C for 1 min; ending with an extension at 72°C for 7 min. The program for 1058F and 2R was similar, but with a starting temperature of 52°C and the last 32 cycles at 48°C.

PCR products were cleaned and sequenced as described using primers waxyF (or rarely 5′old, 181F) and 2R, as well as internal primers 1171R, 1058F, and occasionally 3F (5′-GAT ACC CAA GAG TGG AAC CC-3′; Miller et al., 1999) or 3′N (5′-GCC ATT CAC AAT CCC AGT TAT GC-3′; Peralta and Spooner, 2001) (see fig. 2 in Levin et al., 2005).

trnS-trnG—The chloroplast intergenic spacer between *trnS* and *trnG* was amplified using primers trn S (5′-GCC GCT TTA GTC CAC TCA GC-3′) and trn G (5′-GAA CGA ATC ACA CTT TTA CCA C-3′) of Hamilton (1999). Reactions of 25 μL were done as in Levin et al. (2005), or with 2.5 μL of 10× buffer including 2 mM $MgSO_4$, 0.25 mM dNTPs, 0.36 μM of each primer, 0.625 units of *Taq* polymerase, and 1 μL DNA. The thermal cycler program included an initial denaturing at 94°C for 4 min; 35–40 cycles at 94°C for 45 s, 52°C for 1 min, 72°C for 1 min; ending with an extension at 72°C for 7 min. PCR products were cleaned and sequenced as before, using the same primers as for amplification.

Sequence alignment—Sequences were edited, and a consensus sequence for each species was constructed using Sequencher version 4.2 (Gene Codes, Ann Arbor, Michigan, USA). Species sequences were then aligned manually in SeAl version 2.0 (Rambaut, 2002) and MacClade 4.0 (Maddison and Maddison, 2000). Aligned data sets are available on TreeBASE (S1322, M2318).

Parsimony analyses—The three data sets were analyzed separately (Table 2), and combined. Parsimony analyses were conducted in PAUP* 4.0b10 (Swofford, 2002) using heuristic searches with 100 random addition sequence replicates and tree-bisection-reconnection (TBR) branch swapping. Constant characters were excluded, and gaps were treated as missing data. Following the analysis protocol for large data sets used by Levin et al. (2004), each addition replicate was limited to 200 trees that were greater than or equal to the shortest trees for each replicate. This was necessary due to large numbers of equal length trees. The strength of support for individual tree branches was estimated using bootstrap values (BS) (Felsenstein, 1985) and decay indices (DI) (Bremer, 1988; Donoghue et al., 1992). Bootstrap values were from 500 full heuristic bootstrap replicates, each with 10 random addition sequence replicates. The MulTrees option was not in effect. Decay values for each branch were determined using the PAUP decay index command file in MacClade to prepare a set of trees each with a single branch resolved. To find the shortest trees consistent with each constraint, this file was executed in PAUP* using the heuristic search option with 100 random addition sequence replicates and the MulTrees option disabled. The decay index for each branch is the difference in length between the shortest trees consistent with each constraint and the globally shortest trees.

In the analyses of the ITS and *trnS-trnG* data sets, 134 taxa were included. For *waxy,* 131 taxa were included, as data were missing for three difficult-to-amplify taxa (*S. agrarium*, *S. morellifolium*, and *S. reptans*). In a combined analysis of ITS, *waxy,* and *trnS-trnG,* all 134 taxa were included; thus, for the three aforementioned taxa, the absent region was coded as missing data in the combined analysis. Trees were rooted with *Jaltomata procumbens* in all four analyses.

Data set congruence was tested using partition homogeneity tests (Incongruence length difference, ILD; Farris et al., 1994, 1995) as implemented in PAUP*. ILD tests were conducted with all taxa and the three data sets simultaneously. All pairwise tests were also done, as was a test of *waxy* vs. ITS + *trnS-trnG,* and an analysis of all three data sets with nine taxa excluded (i.e., the three taxa for which *waxy* data were missing as well as six other taxa with conflicting placement across the data sets). These ILD tests were conducted with 200 partition homogeneity replicates (1000 replicates were completed for the ILD test including all taxa and all data sets), each with 10 random addition sequence replicates, TBR branch swapping, MulTrees off, gaps treated as missing data, and constant characters excluded.

Bayesian analysis—A Bayesian analysis was conducted with all three data sets combined using MrBayes version 3.0 beta 4 (Ronquist and Huelsenbeck, 2003). A general time reversible model was used, with gamma-distributed rate variation across sites. This analysis was conducted for 2 million generations with 4 chains. As with the parsimony analyses, *Jaltomata procumbens* was defined as the outgroup. After the analysis was complete, tree length vs. number of generations was graphed in order to determine the point at which tree lengths plateau (Miller et al., 2004). This was estimated to be at ca. 75 000 generations. All trees were loaded into PAUP*, and the trees saved from generations below 75 000 were filtered from the tree set. The remaining trees were summarized as a majority rule consensus tree with posterior probabilities ≥50%.

RESULTS

Nuclear data sets—ITS sequences for 134 taxa ranged in length from 580–655 bp, with an aligned length of 737 characters, including ITS1, the 5.8S rRNA gene, and ITS2. Of these 737 characters, 254 were parsimony-informative (PI) across all 134 taxa, and phylogenetic analysis yielded 1000 most-parsimonious trees (MPTs) of 2023 steps. Despite the high number of PI characters, the ITS data provide little resolution and support for relationships (see Supplemental Appendix S1 accompanying the online version of this article). The strict consensus topology inferred from the ITS data alone does not conflict with the trees shown in Figs. 1–3 except in the placement of *S. polygamum* outside of subgenus *Leptostemonum* (although BS support for this relationship is weak [73%]) and in the sister relationships of *S. anguivi* + *S. incanum* (BS = 99) and *S. felinum* + *S. vestissimum* (BS = 77).

Waxy sequences for 131 taxa ranged in length from 1719–1872 bp, with an aligned length of 1947 characters, from the 5′ region of exon 2 through the 3′ end of exon 10 including eight introns (see Fig. 2 in Levin et al., 2005). Of these characters, 521 were parsimony-informative, and phylogenetic analysis yielded 20 000 (maximum allowed with search strategy) MPTs of 1794 steps. The strict consensus topology in-

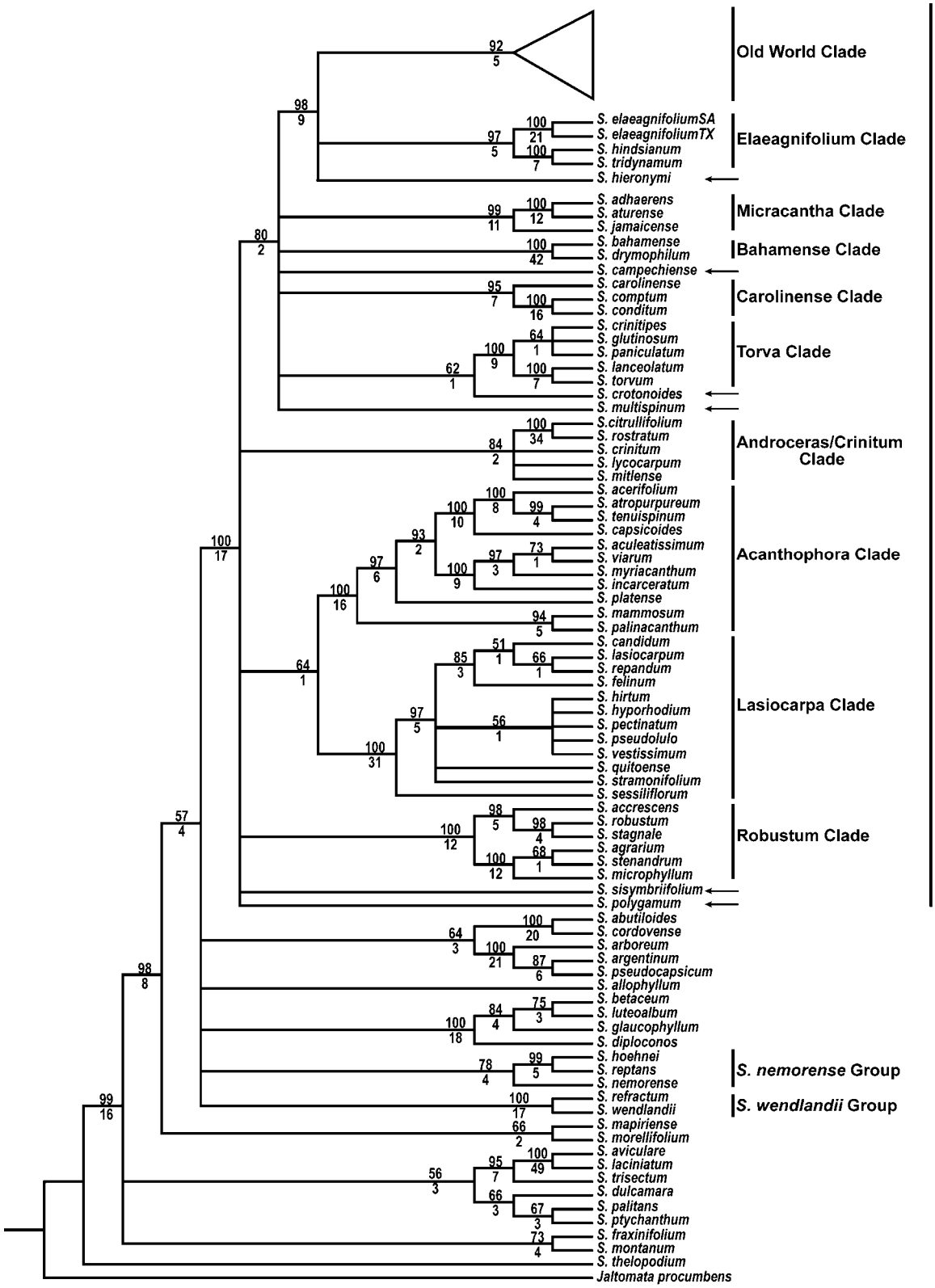

Fig. 1. The parsimony bootstrap consensus tree inferred from the three data sets combined. Bootstrap values ≥50% are shown above the branches, decay indices below. Branches with bootstrap values <50% or with decay indices <1 have been collapsed. Strongly supported clades within subgenus *Lepstostemonum* s.s. are indicated and informally named. For illustrative purposes, the Old World clade is shown as a triangle; see Fig. 2 for the details of relationships of species within this clade. Arrows indicate six taxa that cannot be placed confidently within the 10 named clades.

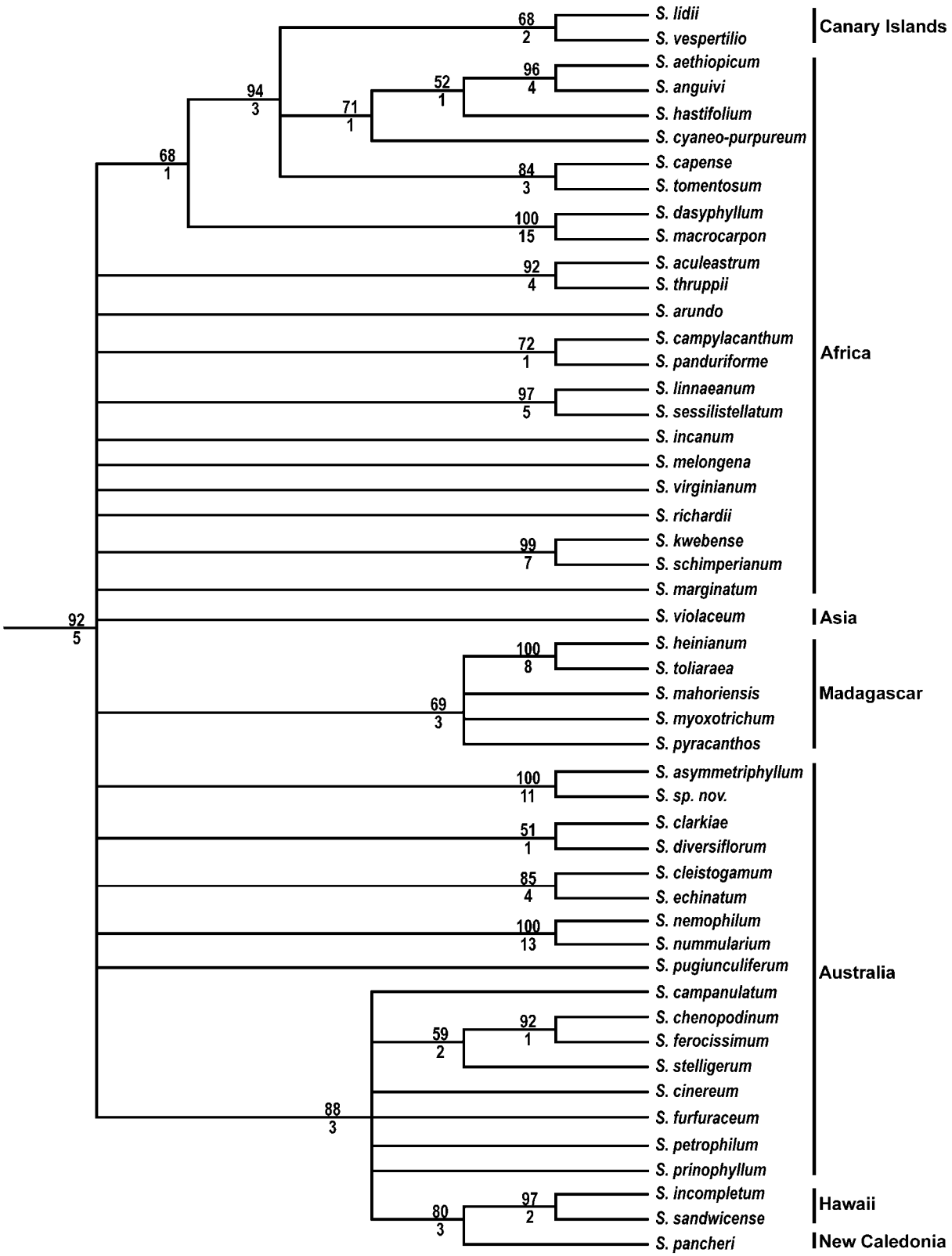

Fig. 2. The Old World clade of the parsimony bootstrap consensus tree inferred from the three data sets combined (Fig. 1). Bootstrap values ≥50% are shown above the branches, decay indices below. Branches with bootstrap values <50% or with decay indices <1 have been collapsed. Geographic regions of various taxon groups are indicated.

ferred from the *waxy* data (see Appendix S2 in Supplemental Data with online version of this article) is much better resolved than the ITS topology and very similar to that from the combined analysis of all three data sets (Figs. 1, 2).

Chloroplast data—The sequences of the *trnS-trnG* spacer region ranged in length from 648–713 bp, with an aligned length of 1004 characters across 134 taxa. Of these characters, 129 were parsimony-informative, and phylogenetic analysis yielded 800 MPTs of 462 steps. Given the low number of PI characters, it is not surprising that these data provide very limited resolution of relationships (see Appendix S3 in Supplemental Data with online version of this article). The only supported difference between the phylogenies inferred from *trnS-trnG* data alone and Figs. 1–3 is that with only *trnS-trnG* there is 81% bootstrap support for *S. hieronymi* as sister to *S. conditum* + *S. comptum* (see Discussion).

All data sets combined—Results of an ILD test comparing all regions suggest that the data sets are not congruent ($P < 0.01$). Further pairwise tests show that the *waxy* data set is incongruent with both other data sets ($P < 0.01$), with only the ITS and *trnS-trnG* data sets being congruent ($P = 0.59$). As discussed before, visual examination of the topologies inferred from each of the regions suggests few differences in relationships, with these topologies differing mainly at the level of resolution. When *S. agrarium*, *S. morellifolium*, and *S. reptans* (the taxa for which *waxy* data were missing) and the few taxa that appeared to differ in placement between the topologies (*S. anguivi*, *S. felinum*, *S. hieronymi*, *S. incanum*, *S. polygamum*, *S. vestissimum*; online Appendices S1–S3) were excluded, the ILD test still suggested incongruence ($P < 0.01$).

Contributing to the significant incongruence may be the large disparity in the size of the partitions (see Table 2), as well as a difference in the substitution rates between the relatively slowly-evolving non-coding *trnS-trnG* region, the coding *waxy* region, and the non-coding, fast-evolving ITS region, resulting in much higher levels of homoplasy in the ITS data (see also Dolphin et al., 2000; Barker and Lutzoni, 2002; Dowton and Austin, 2002). We previously found a similar incongruence of *waxy* in *Solanum* data sets based on chloroplast and nuclear sequences; among *Solanum* section *Acanthophora* and its relatives *waxy* was incongruent with the ITS data, although it was congruent with cp *trnT-trnF* and *trnS-trnG* data (Levin et al., 2005).

Because of the few observed differences in the topologies inferred from the three data sets and the negligible effect on congruence as measured by the ILD test when those taxa that differed in placement among topologies were excluded, all 134 taxa were included in a combined analysis of ITS, *waxy,* and *trnS-trnG* data sets. This analysis included 904 parsimony-informative characters, resulting in 14 200 MPTs of 4447 steps. Despite the large number of MPTs, a consensus of these trees resolves a number of nodes with high support (Figs. 1, 2). Among higher level relationships, *S. thelopodium* (Thelopodium clade [Bohs, 2005]) is at the base of *Solanum*, sister to all other species sampled from the genus (BS = 99; DI = 16). Further, *S. aviculare*, *S. laciniatum* (Archaesolanum clade [Bohs, 2005]), *S. trisectum* (Normania clade [Bohs, 2005]), *S. dulcamara* (Dulcamaroid clade [Bohs, 2005]), *S. palitans*, *S. ptychanthum* (Morelloid clade [Bohs, 2005]), *S. fraxinifolium* (Potato clade [Bohs, 2005]), and *S. montanum* (Regmandra clade [Bohs, 2005]) are sister to the rest of the genus. Within the remainder of *Solanum*, there is strong support (i.e., BS ≥ 90) for the monophyly of subgenus *Leptostemonum* excluding taxa from the *S. wendlandii* (*S. réfractum*, *S. wendlandii*) and *S. nemorense* (*S. nemorense*, *S. hoehnei*, *S. reptans*) groups of Whalen (1984) (BS = 100; DI = 17). Subgenus *Leptostemonum* s.s. (i.e., excluding *S. réfractum*, *S. wendlandii*, *S. nemorense*, *S. hoehnei*, and *S. reptans*) is comprised of several strongly supported clades to which we have assigned informal names:

1. The Robustum clade (BS = 100; DI = 12) includes taxa from the *S. erythrotrichum* (*S. accrescens*, *S. robustum*) and *S. polytrichum* (*S. stagnale*) groups of Whalen (1984), as well as taxa formerly placed within sect. *Acanthophora* (*S. agrarium* and *S. stenandrum*; see Levin et al., 2005). Also included in this clade is the Caribbean Island species *S. microphyllum*, which was not previously placed in a species group by Whalen (1984).
2. The Lasiocarpa clade (BS = 100; DI = 31) includes all species placed by Whalen (1984) in the *S. quitoense* group (i.e., sect. *Lasiocarpa*), and there is weak support for a sister relationship with the Acanthophora clade.
3. The Acanthophora clade (BS = 100; DI = 16) includes most species placed in the *S. mammosum* group by Whalen (1984) (i.e., sect. *Acanthophora*) except for those taxa now included in the Robustum clade (see no. 1).
4. The Androceras/Crinitum clade has moderate support (BS = 84; DI = 2) and includes the *S. rostratum* group of Whalen (1984) (*S. citrullifolium* + *S. rostratum*; BS = 100; DI = 34), the *S. crinitum* group of Whalen (1984) (*S. crinitum*, *S. lycocarpum*), and the previously unplaced Mexican species, *S. mitlense*.
5. The Torva clade (BS = 100; DI = 9) includes all species sampled from the *S. torvum* group of Whalen (1984). Results of the Bayesian analysis (Fig. 3) suggest that *S. crotonoides* is sister to this clade, and although parsimony bootstrap values from the combined analysis only weakly support this relationship (Fig. 1), parsimony analysis of the *waxy* data alone also support *S. crotonoides* as sister to the Torva clade (Appendix S2, with online version of this article).
6. *Solanum carolinense* + *S. comptum* + *S. conditum* comprise a strongly supported Carolinense clade (BS = 95; DI = 7). *Solanum comptum* and *S. conditum* were part of the *S. multispinum* group of Whalen (1984), whereas *S. carolinense* was unplaced.
7. The Bahamense clade is composed of *S. bahamense* + *S. drymophilum* (BS = 100; DI = 42), also placed together by Whalen (1984) in the *S. bahamense* group.
8. The Micracantha clade has strong support (BS = 99; DI = 11), being comprised of the unplaced *S. jamaicense* + *S. aturense* + *S. adhaerens* (the latter two species were placed in the *S. lanceifolium* group of Whalen [1984]). *Solanum adhaerens* has been commonly confused with *S. lanceifolium*, a distinct species from the same species group, and is called *S. lanceifolium* in Whalen's (1984) treatment.
9. The Elaeagnifolium clade (BS = 97; DI = 5) includes *S. elaeagnifolium* accessions from both North and South America, as well as *S. hindsianum* (unplaced by Whalen, 1984) + *S. tridynamum* (*S. vespertilio* group of Whalen [1984]).

10. A large Old World clade is strongly supported (BS = 92; DI = 5) and includes all species of subgenus *Leptostemonum* native to the Old World except for a few derived species from the Lasiocarpa (*S. repandum* and *S. lasiocarpum*) and Acanthophora (*S. aculeatissimum*) clades that may represent recent introductions into the South Pacific and Africa, respectively (see Bohs [2004] and Levin et al. [2005] for details). Included in this clade are the domesticated eggplants *S. aethiopicum*, *S. macrocarpon*, and *S. melongena*.

There are six species that cannot be confidently placed within any of these 10 clades. These include *S. campechiense*, *S. sisymbriifolium*, and *S. polygamum* (all unplaced by Whalen [1984]), *S. hieronymi* and *S. multispinum* (*S. multispinum* group of Whalen [1984]), and *S. crotonoides* (*S. crotonoides* group of Whalen [1984]).

Support for relationships among these 10 clades is limited; however, there is moderate support for the placement of the Robustum, Lasiocarpa, Acanthophora, and Androceras/Crinitum clades outside of a group comprised of the other six clades (BS = 80; DI = 2) (Fig. 1). Further, within these six clades there is strong support for a group comprised of *S. hieronymi* + the Elaeagnifolium and Old World clades (BS = 98; DI = 9).

Bayesian analysis—The consensus phylogeny inferred from a Bayesian analysis of the three data sets combined (Fig. 3) is generally congruent with that inferred from parsimony (Figs. 1, 2), although the Bayesian tree has more resolved nodes (but Fig. 3 is a 50% majority rule consensus tree, rather than a bootstrap consensus tree as shown for parsimony in Figs. 1, 2). In contrast to the results of the parsimony analysis (Fig. 1), the Carolinense, Micracantha, and Torva clades, plus the unplaced species *S. crotonoides* and *S. multispinum*, appear to comprise a monophyletic group with a posterior probability of 100%. In addition, the unplaced *S. sisymbriifolium* appears closely related to the Androceras/Crinitum clade (posterior probability = 97%). Further, relationships within the Old World clade are better resolved (compare Figs. 2 and 3), particularly among the African and Canary Island taxa. The phylogeny inferred by Bayesian analysis also clearly supports the monophyly of the Acanthophora clade + the Lasiocarpa clade (posterior probability = 100%). Within subgenus *Leptostemonum* s.s., the Robustum clade (posterior probability = 100%; Fig. 3) is sister to a clade of all other taxa in the subgenus, a result consistent with the consensus topology inferred from the *waxy* data using parsimony (Appendix S2, with online version of this article).

DISCUSSION

Comparative utility of the three gene regions—All three data sets, including two regions from the nuclear genome and one from the chloroplast genome, resulted in similar topologies. However, in terms of phylogenetic utility, the nuclear GBSSI (*waxy*) gene was the most useful, having both a high percentage of PI characters as well as high consistency and retention indices, suggesting a low level of homoplasy (Table 2). The high information content of this region is likely due to the mix of both noncoding introns and coding exons. The nuclear ITS data set had a higher percentage of PI characters than *waxy*; however, its high level of homoplasy (Table 2) makes ITS less useful than *waxy* for resolving relationships. The *trnS-trnG* spacer region was also phylogenetically informative, but was not as rapidly evolving, having a lower percentage of PI characters than either *waxy* or ITS. However, its utility is enhanced by a low level of homoplasy, similar to that of *waxy*. These results concur with those reported previously for *Solanum* sect. *Acanthophora* (Levin et al., 2005).

Monophyly of subgenus Leptostemonum—Results from both the parsimony and Bayesian analyses of the combined data sets suggest a strongly supported clade that comprises all species of *Solanum* subgenus *Leptostemonum*, excluding the *S. wendlandii* and *S. nemorense* groups of Whalen (1984) (i.e., *Leptostemonum* s.s.). However, our results do not exclude the possibility that these groups are sister to the rest of subgenus *Leptostemonum*. Given the strong molecular support for *Leptostemonum* s.s. (BS = 100; DI = 17; Fig. 1), including a 9-bp, shared deletion in *trnS-trnG*, it may be best to recircumscribe the subgenus to exclude the *S. wendlandii* and *S. nemorense* groups of Whalen (1984). Morphological data support this change. The species of *Leptostemonum* s.s. bear sharp prickles and stellate hairs, whereas the *S. wendlandii* and *S. nemorense* groups have prickles but lack stellate hairs (Fig. 3). Further, the *S. nemorense* group has the long attenuate anthers characteristic of *Leptostemonum* s.s., but species of the *S. wendlandii* group have only weakly attenuate anthers.

Higher level relationships—Given the limited resolution outside of *Leptostemonum* s.s., its closest relatives are unclear. The topology inferred from the Bayesian analysis suggests that either the *S. wendlandii* species group of Whalen (1984) or a clade comprising members of the Brevantherum (including *S. abutiloides* and *S. cordovense*; Bohs, 2005) and Geminata clades (including *S. arboreum*, *S. argentinum*, and *S. pseudocapsicum*; Bohs, 2005) are sister to *Leptostemonum* s.s. However, these relationships have weak support and are not suggested by the combined parsimony analysis (Fig. 1). Data of Bohs (2005) from chloroplast *ndh*F sequences using greater sampling from both the Brevantherum and Geminata clades did not recover a sister relationship between them, and this relationship is only weakly supported (BS = 64) by the combined parsimony analysis (Fig. 1). However, the combined parsimony analysis in the present study (Fig. 1) agrees with Bohs (2005) in placing the following groups as part of a large polytomy together with a strongly supported *Leptostemonum* s.s.: the Brevantherum, Geminata and Cyphomandra (i.e., the clade including *S. diploconos*) clades, the *S. nemorense* and *S. wendlandii* groups, and *S. allophyllum* and *S. mapiriense* (when the node defined by BS = 57 is collapsed; *S. morellifolium* was not included in Bohs [2005]).

Depending on how this polytomy is resolved, alternative scenarios for character evolution in *Solanum* are suggested (Fig. 3). A single origin of prickles in *Solanum* is only supported if the *S. wendlandii* and *S. nemorense* groups form a single clade along with subgenus *Leptostemonum* s.s. Furthermore, if these three groups form a clade, stellate hairs evolved at least twice in *Solanum* (independently in the Brevantherum clade and in *Leptostemonum* s.s.). However, low resolution and support in this part of the tree preclude definitive conclusions at present. A sister relationship between *Leptostemonum* s.s. and the Brevantherum clade may imply that stellate hairs evolved once in *Solanum*, but prickles arose multiple times, once in *Leptostemonum* s.s. and again in the *S. wendlandii* and *S. nemorense* groups. A valuable follow-up to the present

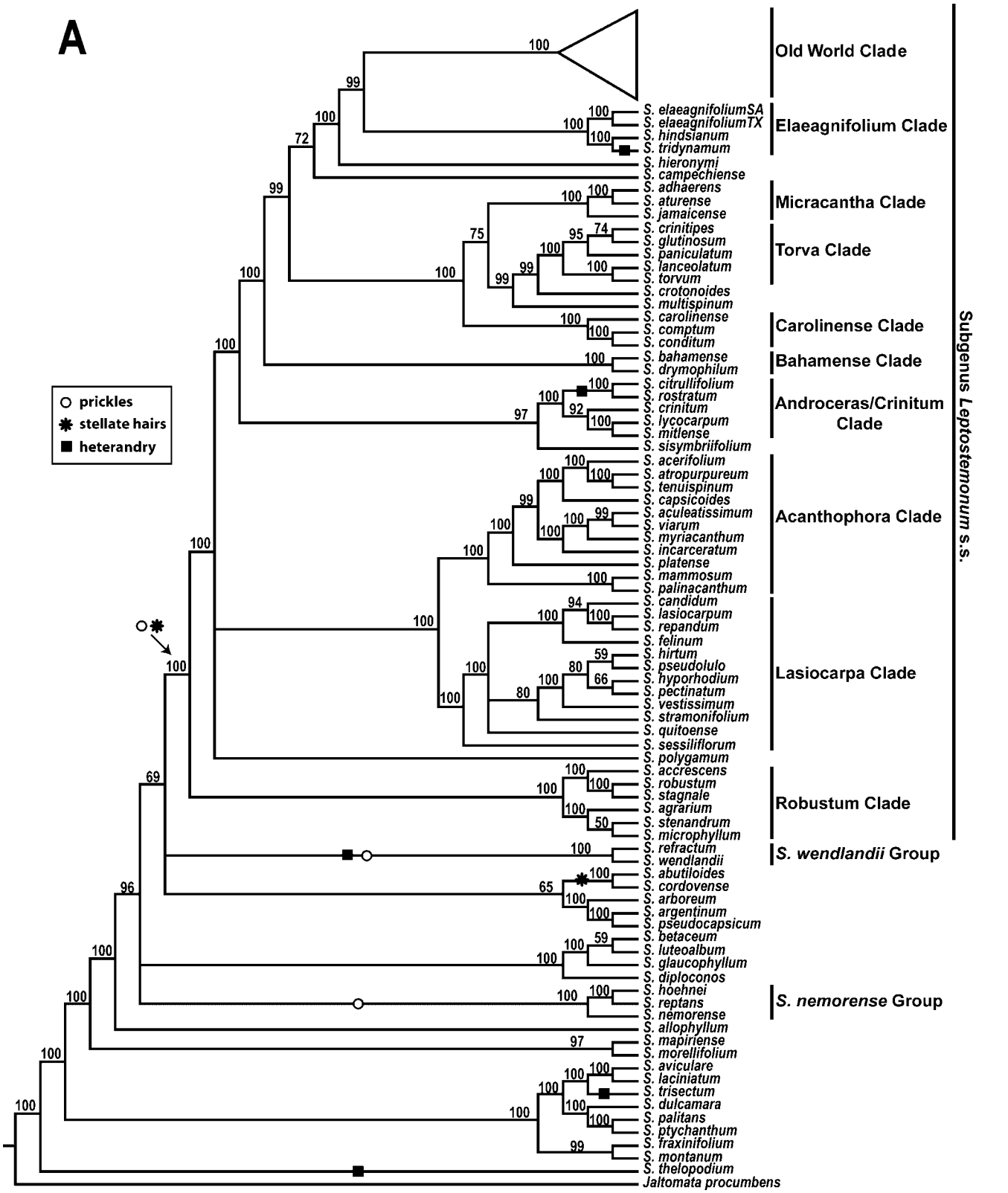

Fig. 3. The 50% majority rule consensus tree inferred from Bayesian analysis of all three data sets combined (A), with the Old World clade shown separately (B). Posterior clade probabilities (>50%) are given above the branches. Informal clade names are shown to the right. The presence of three important characters: prickles, stellate hairs, and heterandry (unequal stamen length) are indicated with symbols.

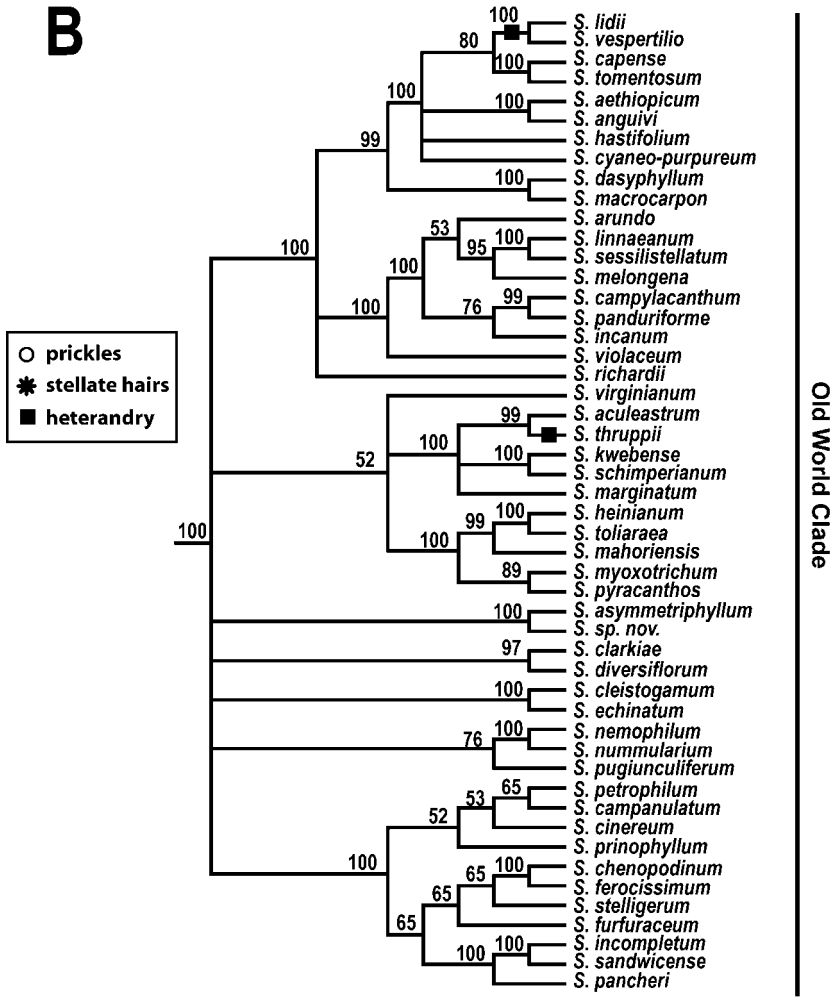

Fig. 3. Continued.

study would be detailed morphological and developmental studies of stellate hairs in *Leptostemonum* s.s. and the Brevantherum clade and prickles in *Leptostemonum* s.s. and the *S. nemorense* and *S. wendlandii* groups to determine whether these structures are homologous in the different clades. Further sampling among *Solanum* species outside of subgenus *Leptostemonum* (L. Bohs et al., unpublished data) may also clarify our understanding of relationships at the base of *Leptostemonum* s.s. and within the genus as a whole.

Relationships within subgenus Leptostemonum—Many of the Whalen (1984) species groups from which we were able to sample multiple taxa appear monophyletic, although further sampling is needed to confirm monophyly of most groups. The *S. quitoense* (Lasiocarpa clade) and *S. mammosum* (Acanthophora clade) species groups were examined in previous molecular analyses (Bohs, 2004, and Levin et al., 2005, respectively). The present results are congruent with these previous studies and concur in excluding *S. agrarium* and *S. stenandrum* from the *S. mammosum* group. The remainder of the species sampled from these two species groups conform to the circumscription of Whalen (1984). Among the other New World taxa, all species sampled from Whalen's *S. torvum* species group form a monophyletic group, comprising our informal Torva clade (Fig. 1). Further, the *S. bahamense* group (i.e., *S. bahamense* + *S. drymophilum*; Bahamense clade) is monophyletic, as is the *S. rostratum* species group (i.e., *S. citrullifolium* + *S. rostratum*; Androceras/Crinitum clade) and the *S. lanceifolium* species group (i.e., *S. adhaerens* + *S. aturense*; Micracantha clade). The *S. multispinum* group of Whalen (1984) does not appear monophyletic; *S. comptum* + *S. conditum* (Carolinense clade) remain sister taxa, but the affinities of the other two species sampled from this species group, *S. hieronymi* and *S. multispinum*, are unclear (Fig. 1). In the case of *S. hieronymi*, the chloroplast data suggest that this species is most closely related to *S. comptum* + *S. conditum* of Whalen's *S. multispinum* group, but the *waxy* data exclude *S. hieronymi* from this clade, and the ITS data do not yield sufficient resolution. The incongruence between the chloroplast and nuclear data sets may suggest hybridization in the pedigree of *S. hieronymi*, which should be investigated using additional data. *Solanum multispinum*, however, remains unplaced in all analyses; given more resolution, this species could be sister to the Carolinense clade (i.e., the present topologies neither support nor contradict this relationship).

In some cases, these data suggest phylogenetic affinities of species not placed in a group by Whalen (1984) or hypothesize relationships among Whalen's species groups. For instance, *S.*

jamaicense was an unplaced species in Whalen (1984), but the molecular data strongly ally it with *S. adhaerens* and *S. aturense* of the *S. lanceifolium* species group (Micracantha clade). Although Whalen (1984) postulated an affinity with the "red-fruited leptostemonums" mainly composed of Old World groups, *S. jamaicense* is morphologically similar to the species of the *S. lanceifolium* group in its scandent habit, recurved prickles, difoliate sympodial units, and deeply stellate corollas. Based on morphology, Nee (1999) also placed *S. jamaicense* together with species of the *S. lanceifolium* group into his expanded section *Micracantha*, but he also included taxa such as *S. nemorense*, which are clearly outside the Micracantha clade in molecular analyses.

Likewise, *S. carolinense* was unplaced in Whalen's (1984) treatment, but molecular data indicate a close relationship with *S. comptum* and *S. conditum*, with all three species comprising the Carolinense clade (Fig. 1). Morphologically, *S. carolinense* is remarkably similar to *S. conditum*, but it is native to the eastern USA, whereas *S. conditum*, *S. comptum*, and other members of Whalen's *S. multispinum* group are native to South America. This disjunction is puzzling, and future studies should focus on confirming the phylogenetic position of *S. carolinense* and investigating how and when this species arrived in North America.

The molecular data offer fairly strong support for the relationship between Whalen's *S. rostratum* and *S. crinitum* species groups. The previously unplaced *S. mitlense* is also part of this Androceras/Crinitum clade. The association of these species in a single clade is unusual from both morphological and biogeographical perspectives. The *S. rostratum* group consists of very prickly annual to perennial plants with highly divided leaves, unequal anthers, enantiostylous flowers, and dryish berries surrounded by a prickly accrescent calyx. The center of diversity of this group is arid regions of the southwest USA and adjacent Mexico. In contrast, the *S. crinitum* group consists of robust shrubs or large forest trees native to humid forests or to cerrado vegetation of South America. Members of the *S. crinitum* group produce some of the largest fruits in *Solanum*, with those of *S. lycocarpum* exceeding 10 cm in diameter. Although the plants are strongly andromonoecious, the flowers are neither heterandrous nor enantiostylous. *Solanum mitlense* occupies an intermediate range in semiarid regions of southern Mexico. In morphology it resembles species of the *S. crinitum* group more than those of the *S. rostratum* group. Although Whalen (1984) speculated that *S. mitlense* may be related to the *S. torvum* group, the molecular data argue against this affinity. Nee (1999) also suggests a possible relationship with the *S. torvum* group or several West Indian *Solanum* species. But, in agreement with the present study, he placed *S. mitlense* together with members of the *S. crinitum* group.

The Bayesian analysis places *S. sisymbriifolium* (unplaced by Whalen) at the base of the Androceras/Crinitum clade with a posterior probability of 97%, but this relationship is not supported in the combined parsimony analysis, in which *S. sisymbriifolium* occupies an unresolved position within *Leptostemonum* s.s. (Figs. 1, 2). Studies of seed surface sculpturing using SEM led Lester et al. (1999) to postulate a close relationship between *S. sisymbriifolium* and the *S. rostratum* group. Nee (1999) considered *S. sisymbriifolium* to be related to *S. campechiense*, another unplaced species in Whalen (1984), but these two species do not form a clade in either the Bayesian or parsimony analyses.

Two of the species groups of Whalen (1984) that are found in both the Old and New Worlds are clearly not monophyletic, with biogeography explaining the true species' affinities. Specifically, the *S. vespertilio* group appears to be comprised of two distinct clades, one of which is native to Mexico (*S. tridynamum*) and belongs within the Elaeagnifolium clade, whereas the other species sampled from the *S. vespertilio* group (*S. lidii* + *S. vespertilio*) comprise a monophyletic group of Canary Island species and are nested within the African taxa (Fig. 2). Whalen (1984) suggested that the Mexican and Canary Island species might comprise distinct phylogenetic groups due to both biogeography and differences in floral morphology. Whereas all four species in the *S. vespertilio* group of Whalen (1984) have heterandrous flowers, the lower anther is longer and upcurved in *S. lidii* and *S. vespertilio*, while the lower three anthers are longer and upcurved in staminate flowers of *S. tridynamum* and *S. azureum* (also from Mexico but not included in the present study). Further, the degree of andromonoecy (i.e., the presence of hermaphroditic and staminate flowers on an individual plant) differs, with the Mexican taxa being highly andromonoecious (only one basal hermaphroditic flower per inflorescence) and the Canary Island species having a greater proportion of hermaphroditic flowers (Whalen, 1984).

The other species group of Whalen (1984) that is found in both the Old and New Worlds is the *S. ellipticum* group. This group contains ca. 35 species, with all but one, *S. elaeagnifolium*, native to Australia. Not surprisingly, our analyses suggest that *S. elaeagnifolium*, native to the Americas, does not belong in the Old World clade with all other members of the *S. ellipticum* group. Rather, this species is sister to *S. tridynamum* and *S. hindsianum*. Nee (1999) also suggested a close relationship among *S. elaeagnifolium*, *S. hindsianum*, and *S. tridynamum*, but he included *S. vespertilio* and *S. liddii* from the Canary Islands in this alliance, similar to the proposal of Whalen described previously. *Solanum elaeagnifolium* has a disjunct distribution, being found in the southwestern USA and Mexico and in southern South America. Its strongly supported sister relationship with the Mexican species *S. tridynamum* and *S. hindsianum* suggests that the native range of *S. elaeagnifolium* could be in North America, with subsequent introduction to South America. The two accessions of *S. elaeagnifolium* used in the present study, one from South America and one from Texas, emerge as sister taxa. Plants of *S. elaeagnifolium* from these disjunct areas should be examined in more detail with morphological and molecular approaches to confirm that they are conspecific and to shed light on their evolutionary history.

Within the large Old World clade, the *S. giganteum* group (*S. kwebense* + *S. schimperianum*; Table 1) appears monophyletic given our limited sampling. Further, there is strong support for the Hawaiian *S. sandwicense* group (*S. incompletum* + *S. sandwicense*; Table 1), which is closely related to the New Caledonian *S. pancheri* (*S. dunalianum* group of Whalen [1984]; Fig. 2). Whalen (1984) also suggested a close relationship between these two species groups due to a shared scarcity of prickles, a similar prickle morphology when present, and similar leaves and fruits. The biogeographical distribution of the taxa in the two species groups further supports a close phylogenetic relationship, with the three species in the *S. sandwicense* group restricted to the Hawaiian Islands, and ca. 20 species that comprise the *S. dunalianum* group found on islands in the South Pacific and in northern Australia.

Among the majority of taxa in the Old World clade, there is not yet sufficient resolution to fully understand relationships among species. The data suggest a Malagasy clade (Figs. 2, 3), and the phylogeny inferred from the Bayesian analysis strongly supports a clade including all of the cultivated eggplant species (*S. aethiopicum*, *S. macrocarpon*, and *S. melongena*) and their wild relatives. However, more data (L. Bohs et al., unpublished manuscript) are necessary to clarify relationships among this diverse, species-rich clade.

Floral evolution—*Solanum* subgenus *Leptostemonum* encompasses much diversity in floral morphologies and breeding systems. Andromonoecy is common across the subgenus and can vary from being "weak," with many hermaphroditic flowers and few staminate ones, to "strong," with usually a single hermaphroditic flower at the base of each inflorescence (e.g., *S. tridynamum*). On this background of andromonoecy, dioecy has apparently evolved multiple times in subgenus *Leptostemonum*. Among New World species, the distantly related *S. polygamum* and *S. crotonoides* are dioecious. There are a number of dioecious species in Australia, but our sampling, including only the dioecious taxa *S. asymmetriphyllum* and a newly described species *Solanum* sp. nov. (Brennan et al., in press), is not sufficient to determine whether the dioecious species comprise a monophyletic group among Australian representatives of the subgenus. Work in progress by C. Martine (University of Connecticut, Storrs, Connecticut, USA) should clarify the evolution of dioecy in Australian *Solanum*.

Heterandry (markedly unequal anthers or stamens within the same flower) is found in several species of subgenus *Leptostemonum*, as well as in some other *Solanum* species outside the subgenus. Heterandry is often, but not always, coupled with enantiostyly (the presence of mirror-image flowers in an inflorescence, with the style deflected opposite the largest anther). Heterandry is clearly homoplastic across *Solanum* (Lester et al., 1999; Bohs and Olmstead, 2001) and has likely evolved at least four times within subgenus *Leptostemonum* (Fig. 3). As discussed, heterandry has evolved twice among the taxa placed by Whalen (1984) in the *S. vespertilio* group, arising once among the Canary Island species and independently in *S. tridynamum* of the Elaeagnifolium clade. Further, heterandry has also evolved in the Androceras/Crinitum clade, with *S. citrullifolium* + *S. rostratum* (and other species in *Solanum* section *Androceras*) having unequal stamens. In addition to the Canary Island species, within the Old World clade *S. thruppii* is also heterandrous. In each case, the heterandrous groups are sister to taxa with stamens equal or nearly so. Further, the *S. wendlandii* group of Whalen (1984), outside of subgenus *Leptostemonum* s.s., exhibits heterandry. This trait is the perfect example of a character where convergence is easily revealed through examination of specific stamen morphology, because the number and location of long vs. short stamens varies across these heterandrous taxa. For instance, the heterandrous flowers of *S. vespertilio*, *S. liddii*, *S. thruppii*, and the species of section *Androceras* have one long stamen and three to four short stamens per flower, whereas the staminate flowers of *S. tridynamum* have three long and two short stamens. Further, the long stamen in *S. vespertilio*, *S. liddii*, and section *Androceras* is due to an elongated anther, with all the filaments relatively equal, whereas *S. thruppii* flowers have subequal anthers, but the longer stamen has an elongated filament. Flowers in the *S. wendlandii* group are similar, with one stamen longer than the rest, largely due to its longer filament.

Conclusions—Results suggest that *Solanum* subgenus *Leptostemonum* is monophyletic when the *S. wendlandii* and *S. nemorense* species groups are excluded. However, the true relationship of these taxa to *Lepstostemonum* s.s. remains unclear. Within *Lepstostemonum* s.s., we have defined 10 clades, some of which correspond to previously circumscribed species groups of Whalen (1984). Increased taxon sampling and more data may help clarify the taxonomic affinities of the six unplaced species, as well as relationships within the large Old World clade.

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APPENDIX. Taxa, localities, vouchers, and GenBank accession numbers for all sequences included in this study. GenBank accession numbers are listed in the following order: ITS, *waxy*, *trnS-trnG*. A dash indicates that the region was not sampled for that accession. BIRM samples have the seed accession number of the Solanaceae collection at the University of Birmingham, UK; Nijmegen accession numbers refer to the Solanaceae collection at the University of Nijmegen, Netherlands. Voucher specimens are deposited in the following herbaria: AD = Plant Biodiversity Centre, Adelaide, Australia; BH = Cornell University; COLO = University of Colorado; CONN = University of Connecticut; F = Field Museum of Natural History; GH = Harvard University; IND = Indiana University; MO = Missouri Botanical Garden; NY = New York Botanical Garden; QCA = Pontificia Universidad Católica del Ecuador; TAN = Parc de Tsimbazaza, Antananarivo, Madagascar; UT = University of Utah; WIS = University of Wisconsin; WTU = University of Washington.

Taxon—Locality, Voucher information; ITS, *waxy*, *trnS-trnG*.

Solanum* subgenus *Leptostemonum

S. accrescens Standl. & C. V. Morton—Costa Rica, *Bohs 2556* (UT); AY996480, AY996375, AY998375. ***S. acerifolium*** *Dunal—Costa Rica, Bohs 2714* (UT); AY561261, AY562949, AY555454. ***S. aculeastrum*** Dunal—Nijmegen 924750119, *Bohs 3251* (UT); AY996481, AY996376, DQ099334. ***S. aculeatissimum*** Jacq.—Nijmegen 924750122, *Cipollini 60* (UT); AY561262, AY562950, AY555455. ***S. adhaerens*** Roem. & Schult.—Costa Rica, *Bohs 2473* (UT); AF244723, AY996377, AY998376. ***S. aethiopicum*** L.—BIRM S.0344, *Olmstead S-74* (WTU); AY996482, AY996378, AY998377. ***S. agrarium*** Sendtn.—Venezuela, *Nee & Whalen 17164* (BH); AY561263,—, AY555456. ***S. anguivi*** Lam.—Nijmegen 974750005, *Cipollini 164* (UT); AY996483, AY996380, AY998379. ***S. arundo*** Mattei—Africa, *Martine 572* (CONN); AY996484, AY996383, AY998382. ***S. asymmetriphyllum*** Specht—Australia, *Symon 17104* (AD); AY996485, AY996384, AY998383. ***S. atropurpureum*** Schrank—Nijmegen 804750109, *Cipollini 91* (UT); AY561264, AY562951, AY555457. ***S. aturense*** Dunal—Costa Rica, *Bohs 2976* (UT); AY996486, AY996385, AY998384. ***S. bahamense*** L.—Nijmegen 944750187, *Bohs 2936* (UT); AY996487, AY996386, AY998385. ***S. campanulatum*** R. Br.—BIRM S.0387, *Olmstead S-78* (WTU); AY996488, AY996388, AY998387. ***S. campechiense*** L.—Costa Rica, *Bohs 2536* (UT); AF244728, AY996389, AY998388. ***S. campylacanthum*** Hochst.—Nijmegen 924750118, *Martine 571* (CONN); AY996489, AY996390, AY998389. ***S. candidum*** Lindl.—BIRM S.0975, *Olmstead S-100* (WTU); AF244722,—,—. Costa Rica, *Bohs 2898* (UT);—, AY562953, AY555459. ***S. capense*** L.—Nijmegen 904750116, *Bohs 2905* (UT); AY996490, AY996391, AY998390. ***S. capsicoides*** All.—Peru, *Bohs 2451* (UT); AY561265, AY562954, AY555460. ***S. carolinense*** L.—USA, *Cipollini SC* (UT); AY996491,—,—. BIRM S.1816, *Olmstead S-77* (WTU);—, AY996392, AY998391. ***S. chenopodinum*** F. Muell.—BIRM S.0813, no voucher; AY996492, AY996393, AY998392. ***S. cinereum*** R. Br.—Nijmegen 904750120, *Bohs 2852* (UT); AY996493, AY996394, AY998393. ***S. citrullifolium*** A. Braun—BIRM S.0127, *Olmstead S-79* (WTU); AY996494, AY996395, AY998394. ***S. clarkiae*** Symon—Australia, *Symon 17109* (AD); AY996495, AY996396, AY998395. ***S. cleistogamum*** Symon—BIRM S.0844, *Olmstead S-80* (WTU); AY996496, AY996397, AY998396. ***S. comptum*** C. V. Morton—Paraguay, *Bohs 3193* (UT); AY996498, AY996399, AY998398. ***S. conditum*** C. V. Morton—Bolivia, *Bohs & Nee 2733* (UT); AY996499, AY996400, AY998399. ***S. crinitipes*** Dunal—Colombia, *Olmstead S-81* (WTU); AY996500, AY996402, AY998401. ***S. crinitum*** Lam.—Nijmegen 924750049, *Bohs 2850* (UT); AY996501, AY996403, AY998402. ***S. crotonoides*** Lam.—Dominican Republic, *Nee 52298* (NY); AY996502, AY996404, AY998403. ***S. cyaneo-purpureum*** De Wild.—Nijmegen 874750010, *Bohs 3164* (UT); AY996503, AY996405, AY998404. ***S. dasyphyllum*** Schumach. & Thonn.—Nijmegen 874750004, *Cipollini 7* (UT); AY996504, AY996406, AY998405. ***S. diversiflorum*** F. Muell.—Nijmegen 914750131, *Bohs 2854* (UT); AY996505, AY996408, AY998407. ***S. drymophilum*** O. E. Schulz—Puerto Rico, *Bohs 2461* (UT); AY996506, AY996409, AY998408. ***S. echinatum*** R. Br.—Australia, *Symon 17102* (AD); AY996507, AY996411, AY998410. ***S. elaeagnifolium*** Cav.—Texas, *Olmstead S-82* (WTU); AF244730, AY996413, AY998412. ***S. elaeagnifolium*** Cav.—Paraguay, *Bohs 3204* (UT); AY996508,—, AY998411. Paraguay, *Bohs 3199* (UT);—, AY996412,—. ***S. felinum*** Whalen—Venezuela, *Benitez de Rojas 8915* (IND); AY996509, AY996414, AY998413. ***S. ferocissimum*** Lindl.—BIRM S.0819, *Olmstead S-83* (WTU); AY996510, AY996415, AY998414. ***S. furfuraceum***

R. Br.—BIRM S.1442, *Olmstead S-84* (WTU); AY996512, AY996417, AY998416. ***S. glutinosum*** Dunal—Nijmegen A34750191, *Bohs 3262* (UT); AY996513, AY996419, AY998418. ***S. hastifolium*** Dunal—Nijmegen 944750142, *Bohs 2906* (UT); AY996514, AY996420, AY998419. ***S. heinianum*** D'Arcy & R. C. Keating—Madagascar, *RHS 275* (TAN); AY996515, AY996421, AY998420. ***S. hieronymi*** Kuntze—Argentina, *Nee et al. 50761* (NY); AY996517, AY996423, AY998422. ***S. hindsianum*** Benth.—Mexico, *Bohs 2975* (UT); AY996518, AY996424, AY998423. ***S. hirtum*** Vahl—Ecuador, *Whalen 730* (QCA); AY263462, AY996425, AY998424. ***S. hoehnei*** C. V. Morton—Brazil, *Folli 1668* (MO); AY996519, AY996426, AY998425. ***S. hyporhodium*** A. Braun & Bouché—Venezuela, *Whalen 717* (BH); AY263461, AY996427, AY998426. ***S. incanum*** L.—Nijmegen 874750008, *Cipollini 81* (UT); AY996520, AY996428, AY998427. ***S. incarceratum*** Ruiz & Pav.—Bolivia, *Nee et al. 51787* (NY); AY561266, AY562955, AY555461. ***S. incompletum*** Dunal—Hawaii, USA, from plant in PTA greenhouse sent by L. Tamimi, no voucher; AY996521, AY996429, AY998428. ***S. jamaicense*** Mill.—BIRM S.1209, *Olmstead S-85* (WTU); AF244724, AY562956, AY555462. ***S. kwebense*** N. E. Br.—Nijmegen 944750162, *Bohs 2849* (UT); AY996522, AY996430, AY998429. ***S. lanceolatum*** Cav.—Costa Rica, *Bohs 2728* (UT); AY996523, AY996432, AY998431. ***S. lasiocarpum*** Dunal—Thailand, *Heiser 8008* (IND); AY263457,—,—. Indonesia, *Ansyar 9605* (IND);—, AY996433, AY998432. ***S. lidii*** Sunding—Nijmegen 934750022, *Bohs 2903* (UT); AY996524, AY996434, AY998433. ***S. linnaeanum*** Hepper & P. Jaeger—Australia, *Cipollini 117* (UT); AY996516, AY996422, AY998421. ***S. lycocarpum*** A. St.-Hil.—Paraguay, *Bohs 3212* (UT); AY996525, AY996435, AY998434. ***S. macrocarpon*** L.—BIRM S.0133, *Olmstead S-88* (WTU); AF244725, AY996436, AY998435. ***S. mahoriensis*** D'Arcy & Rakot.—Madagascar, *Bohs 2576* (UT); AY996526, AY996437, AY998436. ***S. mammosum*** L.—BIRM S.0983, *Olmstead S-89* (WTU); AF244721, AY996438, AY998437. ***S. marginatum*** L. f.—Nijmegen 884750020, no voucher; AY996528, AY996440, AY998439. ***S. melongena*** L.—BIRM S.0657, *Olmstead S-91* (WTU); AF244726, AY562959, AY998440. ***S. microphyllum*** (Lam.) Dunal—Dominican Republic, *Nee 52300* (NY); AY996529, AY996441, AY998441. ***S. mitlense*** Dunal—Mexico, *Whalen & Velasco 825* (BH); AY996530, AY996442, AY998442. ***S. multispinum*** N. E. Br.—Paraguay, *Bohs 3198* (UT); AY996533, AY996444, AY998445. ***S. myoxotrichum*** Baker—Madagascar, *Bohs 2981* (UT); AY996534, AY996445, AY998446. ***S. myriacanthum*** Dunal—Nijmegen 814750043, *Cipollini 83* (UT); AY561267, AY562960, AY555466. ***S. nemophilum*** F. Muell.—Nijmegen A24750100, *Bohs 3254* (UT); AY996535, AY996446, AY998447. ***S. nemorense*** Dunal—Bolivia, *Bohs & Nee 2757* (UT); AY996536, AY996447, AY998448. ***S. nummularium*** S. Moore—Nijmegen 984750119, no voucher; AY996537, AY996448, AY998449. ***S. palinacanthum*** Dunal—Bolivia, *Bohs 3151* (UT); AY561268, AY562961, AY555467. ***S. pancheri*** Guillaumin—New Caledonia, *McKee 41366* (AD); AY996538, AY996450, AY998451. ***S. panduriforme*** E. Mey.—Nijmegen 004750190, *Cipollini 159* (UT); AY996539, AY996451, AY998452. ***S. paniculatum*** L.—Paraguay, *Bohs 3181* (UT); AY996540, AY996452, AY998453. ***S. pectinatum*** Dunal—Ecuador, *Davis & Yost 930* (GH); AY996541,—,—. Ecuador, *Peeke 8512* (IND);—, AY996453, AY998454. ***S. petrophilum*** F. Muell.—Nijmegen 984750189, *Bohs 3255* (UT); AY996542, AY996454, AY998455. ***S. platense*** Dieckmann—Nijmegen 944750217, *Cipollini 182* (UT); AY561269, AY562962, AY555468. ***S. polygamum*** Vahl—Cult. Univ. of CT greenhouse, no voucher; AY996543, AY996455, AY998456. ***S. prinophyllum*** Dunal—Nijmegen 904750171, *Bohs 2725* (UT); AY996544, AY996456, AY998457. ***S. pseudolulo*** Heiser—Colombia, *Plowman et al. 4276* (GH); AY263459, AY562964,—. Nijmegen 824750021, *Miller & Diggle 05* (COLO);—,—, AY555470. ***S. pugiunculiferum*** C. T. White—Australia, *Symon 17112* (AD); AY996545, AY996458, AY998459. ***S. pyracanthos*** Lam.—Cult. USA, *Olmstead S-95* (WTU); AY996546, AY996459, AY998460. ***S. quitoense*** Lam.—Jardín Botanico de Bogotá, Colombia, *Olmstead,* no voucher; AY263460,—,—. Costa Rica, *Bohs 2873* (UT);—, AY562965, AY555471. ***S. réfractum*** Hook. & Arn.—Mexico, *Iltis et al. 29694* (WIS); AY996547, AY996460, AY998461. ***S. repandum*** G. Forst.—Fiji, *Heiser 8215* (IND); AY263466,—,—. Solomon Islands, *Ashley 8627* (IND);—, AY996461, AY998462. ***S. reptans*** Bunbury—Brazil, *de Lima 699* (F); AY996548,—, AY998463. ***S. richardii*** Dunal—Nijmegen 944750152, no voucher; AY996549, AY996462, AY998464. ***S. robustum*** H. L. Wendl.—Argentina, *Bohs 3084* (UT); AY561270, AY562966, AY555472. ***S. rostratum*** Dunal—Colorado, no voucher; AY996550, AY996463, AY998465. ***S. sandwicense*** Hook. & Arn.—Hawaii, *Bohs 2992* (UT); AY996551, AY996464, AY998466. ***S. schimperianum*** Hochst.—BIRM S.1538, *Olmstead S-97* (WTU); AY996552, AY996465, AY998467. ***S. sessiliflorum*** Dunal—Peru, *Dickson 458* (BH) from *Whalen 859* (HUT); AY263455,—,—. Ecuador, *Heiser 8255* (IND);—, AY996467, AY998469. ***S. sessilistellatum*** Bitter—Nijmegen 824750019, *Cipollini 54* (UT); AY996554,—,—. Africa, *Martine 570* (CONN);—, AY996468, AY998470. ***S. sisymbriifolium*** Lam.—Bolivia, *Cipollini 132* (UT); AY561271,—,—. Argentina, *Bohs 2533* (UT);—, AY562967, AY555473. ***S. sp. nov***. Symon—Australia, *Symon 17105* (AD); AY996553, AY996466, AY998468. ***S. stagnale*** Moric.—Brazil, *Carvalho 3213* (IND); AY561272, AY562968, AY555474. ***S. stelligerum*** Sm.—Nijmegen 814750068, no voucher; AY996555, AY996469, AY998471. ***S. stenandrum*** Sendtn.—Brazil, *Irwin et al. 33085* (WIS); AY561273, AY562969, AY555475. ***S. stramonifolium*** Jacq.—Peru, *Whalen & Salick 860* (BH); AY263465, AY562970,—. Peru, *Pickersgill 154* (IND);—,—, AY555476. ***S. tenuispinum*** Rusby—Bolivia, *Bohs 2475* (UT); AY561274, AY996470, AY555477. ***S. thruppii*** C. H. Wright—Nijmegen A34750435, *Bohs 3274* (UT); AY996497, AY996398, AY998397. ***S. toliaraea*** D'Arcy & Rakot.—Madagascar, *Bohs 2982* (UT); AY996557,—,—. Madagascar, *Bohs 2574* (UT);—, AY996472, AY998473. ***S. tomentosum*** L.—Nijmegen 894750127, *Bohs 3107* (UT); AY996558, AY996473, AY998474. ***S. torvum*** Sw.—BIRM S.0839, *Olmstead S-101* (WTU); AF244729, AY562972, AY555478. ***S. tridynamum*** Dunal—Nijmegen 904750179, *Bohs 2977* (UT); AY996559,—,—. BIRM S.1831, *Olmstead S-102* (WTU);—, AY996474, AY998475. ***S. vespertilio*** Aiton—BIRM S.2091, *Olmstead S-103* (WTU); AF244727, AY996476, AY998477. ***S. vestissimum*** Dunal—Venezuela, *Dickson 456* (BH) from *Plowman 13431* (F); AY263467,—,—. Colombia, *Movilla s.n.* (IND) from *Heiser S432*;—, AY996477, AY998478. ***S. viarum*** Dunal—Nijmegen 934750190, *Cipollini 67* (UT); AY561275, AY562973, AY555480. ***S. violaceum*** Ortega—Nijmegen 924750100, *Bohs 3093* (UT); AY996560, AY996478, AY998479. ***S. virginianum*** L.—Nijmegen 934750032, *Cipollini 17* (UT); AY996561, AY996479, AY998480. ***S. wendlandii*** Hook. f.—BIRM S.0488, no voucher; AF244731, AY562974, AY555481.

Solanum* outside subgenus *Leptostemonum

S. abutiloides (Griseb.) Bitter & Lillo—BIRM S.0655, *Olmstead S-73* (WTU); AF244716, AY562948, AY555453. ***S. allophyllum*** (Miers) Standl.—Panama, *Bohs 2339* (UT); AF244732, AY996379, AY998378. ***S. arboreum*** Dunal—Costa Rica, *Bohs 2521* (UT); AF244719, AY996381, AY998380. ***S. argentinum*** Bitter & Lillo—Argentina, seeds from *Zygadlo 100, Bohs 2539* (UT); AF244718, AY996382, AY998381. ***S. aviculare*** G. Forst.—BIRM S.0809, no voucher; AF244719, AY562952, AY555458. ***S. betaceum*** Cav.—Bolivia, *Bohs 2468* (UT); AF244713, AY996387, AY998386. ***S. cordovense*** Sessé & Moc.—Costa Rica, *Bohs 2693* (UT); AF244717, AY996401, AY998400. ***S. diploconos*** (Mart.) Bohs—Brazil, *Bohs 2335* (UT); AY523890, AY996407, AY998406. ***S. dulcamara*** L.—No voucher, Cult. Michigan USA; AF244742, AY996410, AY998409. ***S. fraxinifolium*** Dunal—Costa Rica, *Bohs 2558* (UT); AY996511, AY996416, AY998415. ***S. glaucophyllum*** Desf.—No voucher; AF244714, AY996418, AY998417. ***S. laciniatum*** Aiton—New Zealand, *Bohs 2528* (UT); AF244744, AY996431, AY998430. ***S. luteoalbum*** Pers.—BIRM S.0042, *Bohs 2337* (UT); AF244715, AY562957, AY555463. ***S. mapiriense*** Bitter—Bolivia, *Nee & Solomon 30305* (UT); AY996527, AY996439, AY998438. ***S. montanum*** L.—Nijmegen 904750205, *Bohs 2870* (UT); AY996531, AY996443, AY998443. ***S. morellifolium*** Bohs—Ecuador, *Cerón & Cerón 4549* (MO); AY996532,—, AY998444. ***S. palitans*** C. V. Morton—BIRM S.0837/70, *Bohs 2449* (UT); AF244739, AY996449, AY998450. ***S. pseudocapsicum*** L.—BIRM S.0870, no voucher; AF244720, AY562963, AY555469. ***S. ptychanthum*** Dunal—Chicago, *Olmstead S-94* (WTU); AF244735, AY996457, AY998458. ***S. thelopodium*** Sendtn.—Bolivia, *Nee & Bohs 50858* (NY); AY996556, AY996471, AY998472. ***S. trisectum*** Dunal—France, *Bohs 2718* (UT); AF244733, AY996475, AY998476.

Outgroup

Jaltomata procumbens (Cav.) J. L. Gentry—Mexico, *Davis 1189A*; AF244710, AY996374, AY998374.