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Color by Numbers: Nuclear Gene Phylogeny of *Jaltomata* (Solanaceae), Sister Genus to *Solanum*, Supports Three Clades Differing in Fruit Color

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Abstract—DNA sequences from the nuclear gene *waxy* were used to assess phylogenetic relationships within *Jaltomata*, a group of approximately 60 species from Central and South America. Phylogenetic analyses identify two primary groups: a morphologically diverse group from western South America, characterized by orange fruits, and a primarily Mesoamerican clade with black/purple fruit and little morphological diversity. We also identify an early-diverging lineage of *Jaltomata* species with red fruits, which is sister to the rest of the genus. Ancestral character state reconstruction supports a view of the common ancestor of the genus originating in South America and having rotate corollas similar to many species of *Solanum*. In addition, we infer independent colonizations of lomas habitats by *Jaltomata* species and show a correlation between red nectar production and campanulate floral form in multiple lineages, suggesting a common evolutionary syndrome related to pollination.

Keywords—GBSSI, molecular systematics, nuclear DNA, phylogeny, *waxy*.

Molecular phylogenetic studies identify *Jaltomata* as the sister group to *Solanum* (Olmstead and Palmer 1992; Olmstead et al. 1999; Hu and Saedler 2007; Weese and Bohs 2007; Olmstead et al. 2008); the two genera together comprise tribe Solaneae (Olmstead et al. 2008). With about 60 species, *Jaltomata* is a much smaller clade than *Solanum*, which includes approximately 1,500 species. The two genera are morphologically distinct: *Jaltomata* produces floral nectar and has longitudinal anther dehiscence whereas *Solanum* lacks floral nectar and possesses anthers with terminal pores. These differences in floral characters are expected to be causally related to selection by pollinators. *Solanum* is bee-pollinated (Eickwort 1967; Buchmann 1983; Knapp 1986; Sazima et al. 1993); *Jaltomata* pollination has not been studied extensively, although *Jaltomata* species are visited by bees (Eickwort 1967; Williams 1985) and hummingbirds (Mione and Leiva G., field observation).

Jaltomata is a much more diverse group than previously thought (e.g. four species in D'Arcy 1979 and 10 species in D'Arcy 1991). The expanded diversity recognized at present derives from both the recognition of several species assigned to different genera (e.g. *Saracha*) and all of *Hebecladus* being reassigned to *Jaltomata* (Hunziker 1979; Mione et al. 1993, 1994), as well as the discovery of many new species. (Leiva G. et al. 1998, 2007a, 2007b, 2008; Mione et al. 1993, 2000a, 2000b, 2004, 2007, 2008). *Jaltomata* exhibits an array of vegetative and floral morphology; much of this character diversity has come to light only recently because many species are narrow endemics and found in remote, historically under-collected locations in the Andes of South America.

Two subgroups of *Jaltomata* have been recognized on the basis of morphology (Mione and Anderson 1996) and a cpDNA restriction site analysis, in which 14 species were sampled, along with representatives of several other genera of Physaleae, then assumed to be among the closest relatives of *Jaltomata* (Mione et al. 1994). The latter study also showed that species previously assigned to *Hebecladus* and *Saracha* belonged with *Jaltomata*. The black/purple-fruited subgroup includes about 10 species distributed from the southwestern U. S. A. to Bolivia (Mione and Yacher 2005). These are primarily herbaceous plants with little or no secondary growth, without periderm, and with pale-green rotate corollas. This subgroup includes two widespread species (*J. procumbens* and *J. repandidentata*) of southern North America, Central America, and western South America, and about eight narrowly distributed species of Mexico and Central America.

In contrast, the red/orange-fruited subgroup includes about 50 species distributed in the Andes from Venezuela to Bolivia, the desert along the coast of Peru, the Galápagos Islands (D'Arcy 1982a, 1982b), and the Greater Antilles (*J. antillana*; Mione 1992). These are mostly shrubs with a conspicuous periderm, but a few are herbaceous. In this group, corolla form and color vary markedly. Two species, *J. aspera* and a new, undescribed species (*J.* "hummingbird" in this study), share a unique stigma and style morphology and possess a bowl-like floral structure, formed by the fused bases of the stamens, on which red/orange nectar pools.

Red nectar color is exceedingly rare (Hansen et al. 2007), but occurs in 13 species of *Jaltomata* from Peru and Bolivia (Mione and Anderson 1996). Three other species normally producing clear nectar have been observed producing red/orange nectar at least once, either in the field or in cultivation (e.g. Mione et al. 2001).

At least six *Jaltomata* species, including two with red nectar, grow in unique desert-fog areas known as lomas. These distinctive areas occur from northern Peru to northern Chile, in places where coastal deserts are punctuated by small mountains and slopes are high enough to be bathed seasonally in ocean fog (Rundel et al. 1991). Where fog hits the near-shore slopes and mountaintops, moisture drips off the vegetation and rocks creating verdant oases known as lomas communities. These are virtual islands surrounded by hyperarid desert and are separated from the much higher Andes to the east (Dillon 1997, 2005). Many species that live in lomas are endemic to that habitat (Rundel et al. 1991). Of the four lomas species sampled, only *J. aspera* occurs in both the lomas and the Andes. Diverse corolla forms, nectar color variation, and differences in leaf deciduousness support a hypothesis of colonization of the lomas by different Andean progenitors.

While *Solanum* is the largest and most economically important genus of Solanaceae (including tomatoes, potatoes, and eggplant), fruits of most *Jaltomata* species also are consumed (Altschul 1973; Díaz 1976; Williams 1985; Davis 1986; Schultes

and Raffauf 1990; Laferrière et al. 1991; Mione and Bye 1996). The fruits are round, fleshy berries ranging from purple, black, green, to orange or red at maturity. Green-fruited species are known from both the red/orange-fruited and black/purple-fruited subgroups of *Jaltomata*. Green fruits are produced by some, but not all, collections of *J. chihuahensis* (Mione and Bye 1996), an unnamed race of *J. procumbens* (Williams 1985) represented in this study as *J.* "green fruit," *J. lezamae*, and *J.* "hummingbird."

The lack of a phylogeny for the majority of species of *Jaltomata* and the extensive floral diversity, especially in corolla tube length and nectar color, within *Jaltomata*, in contrast to the relatively more uniform flower types and absence of nectar in its sister group, *Solanum*, prompted this study. Our objectives were: 1) to test the validity of the two main subgroups within the genus identified by previous studies and 2) to infer the evolution of morphological traits within *Jaltomata*.

We focus on a nuclear gene, because previously published cpDNA gene sequences for *Jaltomata* show low levels of divergence between species. Low copy nuclear genes like *waxy* have been used successfully at the interspecific level to resolve phylogenetic relationships when cpDNA exhibits low levels of divergence (Sang 2002; Hughes et al. 2006). The *waxy* gene was chosen for this study based on phylogenetic studies within *Solanum*, the sister genus to *Jaltomata*, which indicated the utility of using *waxy* for resolving species relationships (Peralta and Spooner 2001; Levin et al. 2006; Weese and Bohs 2007; Spooner et al. 2008). We then infer ancestral state reconstructions to focus on the evolution of five traits: floral shape, colored nectar production, fruit color, habitat, and habit.

Materials and Methods

Data Collection—A total of 68 accessions representing 50 *Jaltomata* taxa, including eight new and unnamed taxa, were included in this study (Appendix 1). Five species were selected as outgroups: *Physalis alkekengi*, *Witheringia solanacea*, *Lycianthes heteroclita* to sample the diversity from the sister clade to Solaneae (Olmstead et al. 2008), and *Solanum lycopersicum* and *S. melongena* to represent each of the two large *Solanum* clades (Weese and Bohs 2007).

Molecular Techniques—Total genomic DNA was extracted from field-collected, silica-gel dried tissue using the modified 2 × CTAB method (Doyle and Doyle 1987) and purified using Wizard minicolumns (Promega, Madison, Wisconsin). The polymerase chain reaction (PCR) was performed to amplify the region spanning exons 2–13 of the gene for Granule Bound Starch Synthase I (GBSSI gene, commonly referred to as *waxy*). Amplifications were conducted in 25 µL volumes with annealing temperatures of 50–55°C using primers 2F, 13R1 and 13R2 from Table 1. Amplified *waxy* products were cleaned by precipitation from a 20% polyethylene glycol 8000/NaCl solution and washed with 70% EtOH prior to sequencing. Both strands were directly sequenced using either DYEnamic ET Terminator (GE Healthcare, Piscataway, New Jersey) or BigDye Terminator v3.1 (Applied Biosystems Inc, Foster City, California) cycle sequencing kits on ABI model 377 or 3100 automated DNA sequencers. *Jaltomata* specific PCR primers and internal primers (Table 1) used for sequencing were designed from previously published *Solanum* (AP009280, X58453) and *Jaltomata* sequences (DQ169009, AY996374, AY875405). Previously designed primers for Solanaceae were also used for sequencing (Yuan et al. 2006; Table 1). Amplification products for which length polymorphism was detected during direct sequencing were cloned using the TOPO TA cloning kit for sequencing (Invitrogen, Carlsbad, California), and four to six clones were sequenced for each taxon. Sequence data were proofed, edited, and contigs assembled using Sequencher v.4.7 (Gene Codes Corp., Ann Arbor, Michigan). Generated sequences were deposited in GenBank under accession numbers GU256289-GU256358 as listed in Appendix 1, and the aligned dataset with gap codes is deposited in TreeBASE (study number S10388).

Phylogenetic Analyses—Sequences were manually aligned using the program MacClade 4.08 OSX (Sinauer Associates, Inc, Sunderland, Massachusets). Parsimony-informative gaps were coded as presence/absence characters using simple gap coding (Simmons and Ochoterena 2000; Graham et al. 2000). When multiple accessions of the same taxon had identical sequences (summarized in Table 2), only one sequence was included in our phylogenetic analyses.

Phylogenetic analyses were performed using maximum likelihood and Bayesian inference methods. DT-Model Select (Minin et al. 2003) was used to determine the best-fit model of sequence evolution. The HKY (Hasegawa et al. 1985) with discrete gamma distributed rate variation (Yang 1994) model of sequence evolution was indicated as the best-fit to the data. The same model was supported as the best-fit in Modeltest 3.7 by both the Akaike information criterion and Bayesian information critertion (Posada and Crandall 1998).

Maximum likelihood (ML) analyses were performed using the program GARLI version 0.96b (Zwickl 2006). Forty searches were performed on the CIPRES cluster (Miller et al. 2009) under default parameters (including four categories of discrete approximation of gamma-distributed rate heterogeneity, starting trees created by stepwise-addition with 50 attachment branches evaluated for each taxon, branch-length optimization started at 0.5, reduced 20 times to a minimum of 0.01). To verify convergence,

Table 1. *Jaltomata* primers used for PCR and sequencing of *waxy*. (J) – primers designed specifically for *Jaltomata*.

name		Sequence (5′→3′)	source
waxy_2F	(J)	GGATACTAGCGTTGCGGTTGAG	
waxy_5F		CAGGCAGCACTAGAGGCACC	Yuan et al. 2006
waxy_5R		GGTGCCTCTAGTGCTGCCTG	Yuan et al. 2006
waxy_7F	(J)	CCGATTTGCTTTCTCTGACTTCC	
waxy_7R		ATCGGCCTTGGTAGGCAATGT	Yuan et al. 2006
waxy_8F		GCATGGATACMCAAGAGTGG	Yuan et al. 2006
waxy_8R		ACTCTTGTGTATCCATGCCAT	Yuan et al. 2006
waxy_10F	(J)	AACAGCTTGAAGTGTTGTATCCTGAC	
waxy_10R	(J)	CATTGAACTTTGCCACTCCTTTAGC	
waxy_11F	(J)	GAGTCAGGTGCCAATCTGTGC	
waxy_11R	(J)	AGTGTCAACAAGTCCACCAGTC	
waxy_12R	(J)	CATCTGGGTCAACAACATCGCAC	
waxy_13R2	(J)	TCTCCCATTTCTTGGCAGGTTC	
waxy_13R1	(J)	CATTTAGGGAGTGGCTACATTTTCC	

Table 2. When numerous collections were sampled within one species, some were identical in DNA sequence for exons 2–12 of the *waxy* gene. To simplify the phylogenetic trees, taxa were removed from the final analyses that were identical to the listed GenBank accessions: species, GenBank number, collection locality, and accession number which appears in the phylogenetic trees are listed.

Species	GenBank No.	Collection locality	Identical to
J. bicolor	GU256289	Peru, Ancash, Aija	
	GU256290	Peru, Ancash, Bolognesi	GU256289
J. dentata	GU256292	Peru, Lima, Huarochiri	GU256293
	GU256293	Peru, Lima, Canta	
J. procumbens	GU256339	Costa Rica	
	GU256340	Costa Rica (epiphyte)	
	GU256341	Costa Rica, Alajuela	GU256340
	GU256342	Guatemala, Quezaltenango	
	GU256343	Mexico, Oaxaca	
	GU256344	Mexico, Chiapas	
J. repandidentata	GU256351	Nicaragua, Granada	GU256355
	GU256352	Mexico, Veracruz	GU256355
	GU256353	Costa Rica, Puntarenas	GU256355
	GU256354	Costa Rica, San Jose prov.	GU256355
	GU256355	Costa Rica, Puntarenas	
J. salpoensis	GU256335	Peru, Amazonas	
	GU256336	Peru, La Libertad	GU256335
J. sanchez-vegae	GU256318	Peru, La Libertad	GU256319
	GU256319	Peru, Cajamarca	
J. sinuosa	GU256304	Peru, Amazonas	GU256305
	GU256305	Peru, Cajamarca	

20 searches were started from stepwise-addition trees and 20 from random trees. Free model parameters were estimated for each search replicate and automatically terminated after 20,000 generations without improvement in the topology score. One thousand bootstrap (Felsenstein 1985) repetitions were performed with the same parameters as above, but with two replicates per search and all starting trees created by stepwise-addition. Each pseudoreplicate was automatically stopped after 10,000 generations without improvement in the topology score and bootstrap proportions were calculated by computing a majority rule consensus tree in PAUP* (Swofford 2002).

Bayesian phylogenetic analyses were performed using the program MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003). Gap data were included as a second partition using the binary model as implemented in MrBayes, coding set to variable, and model-specific parameters permitted to estimate parameters specific to each model. Analyses consisted of three parallel runs, each of 7,500,000 generations from a random starting tree using default priors (all topologies equally probable, branch lengths modeled under an exponential distribution with parameter 10, a uniform (0.0, 200) distribution for the gamma shape parameter, a Beta (1.0, 1.0) distribution for the transition and transversion rates, and a flat (1, 1, 1, 1) Dirichlet distribution for the state frequencies), with four Metropolis-coupled Markov chains sampled every 100 generations. Three of the chains were incrementally heated with a temperature of 0.15. The appropriate temperature value was determined during preliminary runs to allow swap rates between chains to exceed the minimum suggested rate of 0.10. Convergence was determined when the average standard deviation of split frequencies between runs stayed below 0.01 and graphically checked using AWTY (Nylander et al. 2008). For each run the first 25% of all generations were discarded as burn-in. The remaining samples from each run were grouped as the posterior distribution of trees. A majority-rule consensus tree showing all compatible partitions and average branch lengths was made in MrBayes from the posterior distribution of trees to recover the posterior probabilities for each clade.

Published cpDNA genes were compared to divergence levels within *waxy* for *Jaltomata* and *Solanum*. *Jaltomata sinuosa*, *J. procumbens*, and *Solanum lycopersicum* were compared for *ndhF* (AF500835, U47429, U08921) and *trnT-trnF* (DQ180418, DQ180419, DQ180450) (Weese and Bohs 2007); *Jaltomata dentata* (EF438985), *J. hunzikeri* (EF438939), and *Solanum lycopersicum* (EF438904) (Hu and Saedler 2007) were compared for *matK*. *Jaltomata procumbens* (GU256344), and *J. sinuosa* (GU256305) from this study were compared to *Solanum lycopersicum* (AP009280) for *waxy*. Substitution number and uncorrected pairwise distance were calculated using PAUP* (Swofford 2002).

Ancestral states were reconstructed in Mesquite 2.7.1 (Maddison and Maddison 2009). Five morphological traits and species distribution were scored as categorical data with multiple states. Four states were assigned to fruit color: orange, green, purple/black, and red. Five corolla forms were recognized: broadly campanulate, urceolate-tubular, short tubular, crateriform, and rotate. Nectar color has three states: red to orange, clear and orange (trait varies within the species), and clear. Four geographic regions were assigned: South America, widespread, Mexico and Central America, and the Greater Antilles. Three states were recognized for habit: woody, suffruticose, and herbaceous. Ancestral states were reconstructed on the Bayesian consensus tree using a parsimony model with the unordered states assumption as implemented in Mesquite. To increase readability, outgroups were removed from figures. For *Solanum*, states were scored as follows: corolla form = rotate, geography = South American, and habit = herbaceous.

Results

The *waxy* sequences from the end of exon 2 through the beginning of exon 13 were aligned for all *Jaltomata* species and five outgroup species. Three physaloid taxa and the *S. melongena* sequences were available only from exons 2–10 plus a portion of intron 10. Individual *Jaltomata* sequence lengths ranged from 2,405–2,457 bases; numerous gaps of only a few bases were introduced to create a total alignment of 2,598 bases. Thirteen *Jaltomata*-specific gaps were included in the Bayesian analyses as binary characters. In the aligned dataset, 287 DNA positions were scored as missing data out of 142,115 total positions (0.20%) for 58 *Jaltomata* gene sequences.

Bayesian inference and ML analyses produced similar results in topology but differed in support values at some branches. Figure 1 depicts a strict consensus tree of the 13 best scoring trees from ML searches (-7,554.4935). Figure 2 contains a consensus tree showing inferred branch lengths from MrBayes. The overall topology between the two analyses is similar and the fully resolved consensus tree from MrBayes in Fig. 2 is compatible with the strict consensus ML tree in Fig. 1. Support values are included for the backbone of the tree when branches resolved in the Bayesian consensus tree in Fig. 2 are not present in the strict consensus of ML trees in Fig. 1.

The earliest-diverging clade (clade 1) of *Jaltomata antillana* and *J. auriculata* forms a group (98% ML bootstrap value (BS)/1.00 posterior probability (PP) from MrBayes) that is sister to the rest of *Jaltomata* with 72 BS and 0.40 PP support. Two other clades are resolved from both analyses. All of the black/purple-fruited *Jaltomata* (herbaceous, rotate corollas; Fig. 3a) from Mexico and Central America form clade 2 (93 BS/1.00 PP). Clade 3 is morphologically diverse and is obtained in the Bayesian tree (Fig. 2) and some of the ML trees (Fig. 1) with low support (38 BS/0.25 PP).

The main difference between the trees of Figs. 1 and 2 is the resolution of the lineage comprising *Jaltomata oppositifolia* and *J.* "SanMiguel" (clade 3a), which is unresolved with respect to the other lineages of clade 3 and clade 2 in Fig. 1, but is part of a weakly supported clade 3 in the Bayesian consensus tree (Fig. 2). Although support values for this region of the tree are low, six of the thirteen best-scoring ML trees support clade 3a as the sister to the rest of the species in clade 3 while the other seven best-scoring trees fail to resolve the relationship between clade 3a, clade 2, and the other species of clade 3 (Fig. 1). Thus, despite the weak support, there are no optimal trees in either search that contradict the existence of clade 3.

The other subclades of clade 3 receive high Bayesian support values but low ML bootstrap values, except for clade 3b. Clade 3b is a well-supported group of *J.* "purple ring" (Fig. 3d) and *J. salpoensis* (100 BS/1.00 PP). Clades 3c and 3d form a well supported clade (78 BS/1.00 PP). These two sister clades encompass the majority of *Jaltomata* species and most of the diversity in corolla form and nectar color (Fig. 4b). Clades 3c and 3d include 17 and 19 taxa, respectively, and each group has high Bayesian support, but low ML BS (3c - 24 BS/0.91 PP, 3d - 42 BS/1.00 PP).

Gene divergence within *Jaltomata* and between species of *Jaltomata* and *Solanum* (Solaneae) is summarized in Table 3 for *waxy* and published cpDNA genes. Within *Jaltomata*, *waxy* contains more than twice as many substitutions per character (0.012) as the most divergent chloroplast region, *trnT-trnF* (0.0051).

Ancestral State Reconstruction—Ancestral character state reconstructions are depicted in Figs. 4 and 5. The number of steps for each parsimony-based character reconstruction is listed in Table 4.

Discussion

Clade 1—The earliest diverging *Jaltomata* lineage is represented by two species, *Jaltomata antillana* (Greater Antilles) and *J. auriculata* (Andes), which are sister to the remaining species of the genus (Fig. 1). These two species (and another for which material was unavailable, *J. sanctae-martae*) share a unique combination of traits: white, rotate corollas (Fig. 4b),

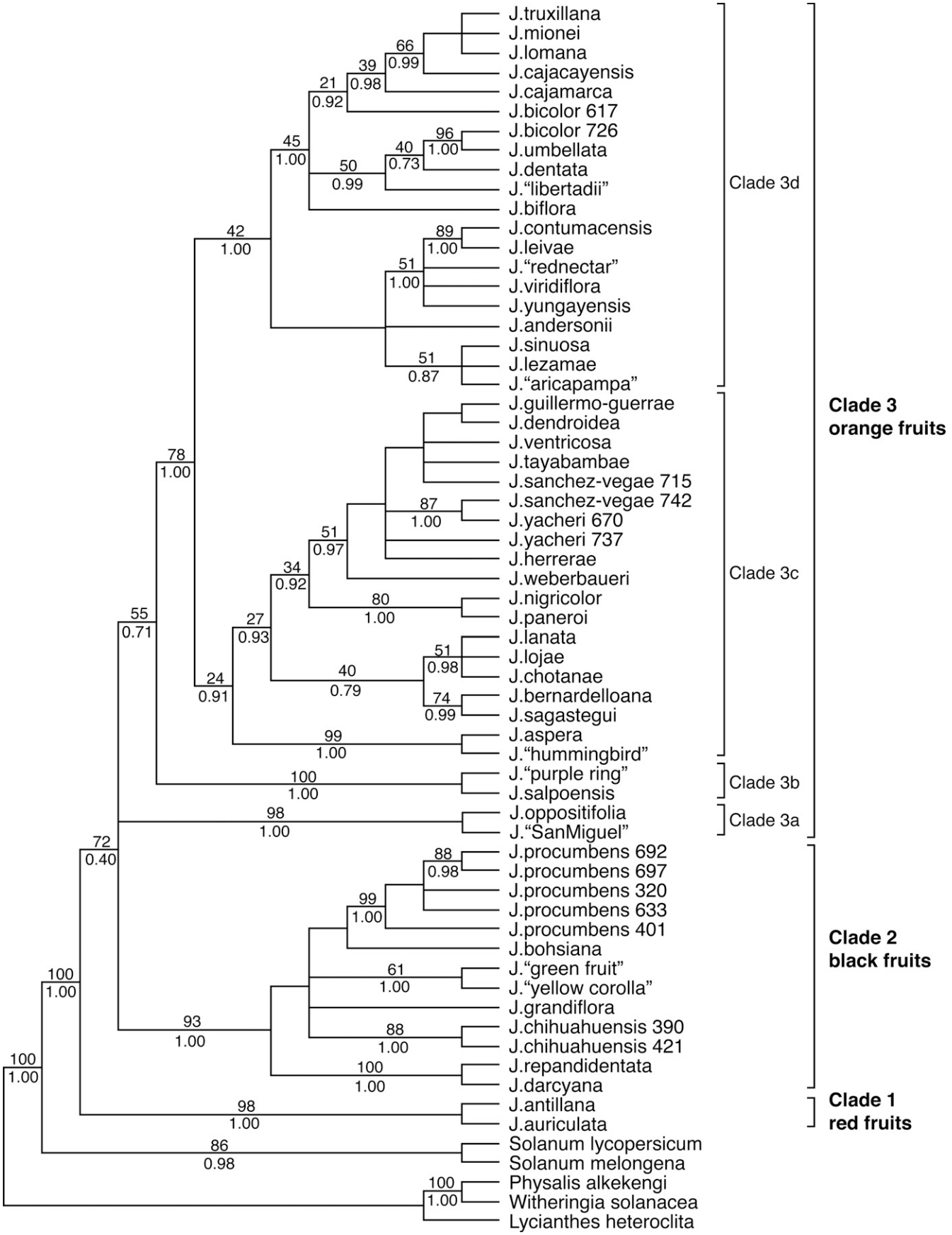


FIG. 1. Strict consensus of 13 best-scoring trees from GARLI maximum likelihood (ML) analyses. Maximum likelihood bootstrap percentages of 1,000 pseudoreplicates are included above branches and posterior probabilities from Bayesian inference are below branches to show support values ≥ 70% for individual clades. Clade 3 is not supported by all optimal ML trees, but is consistent with all ML trees and is supported by the Bayesian analysis.

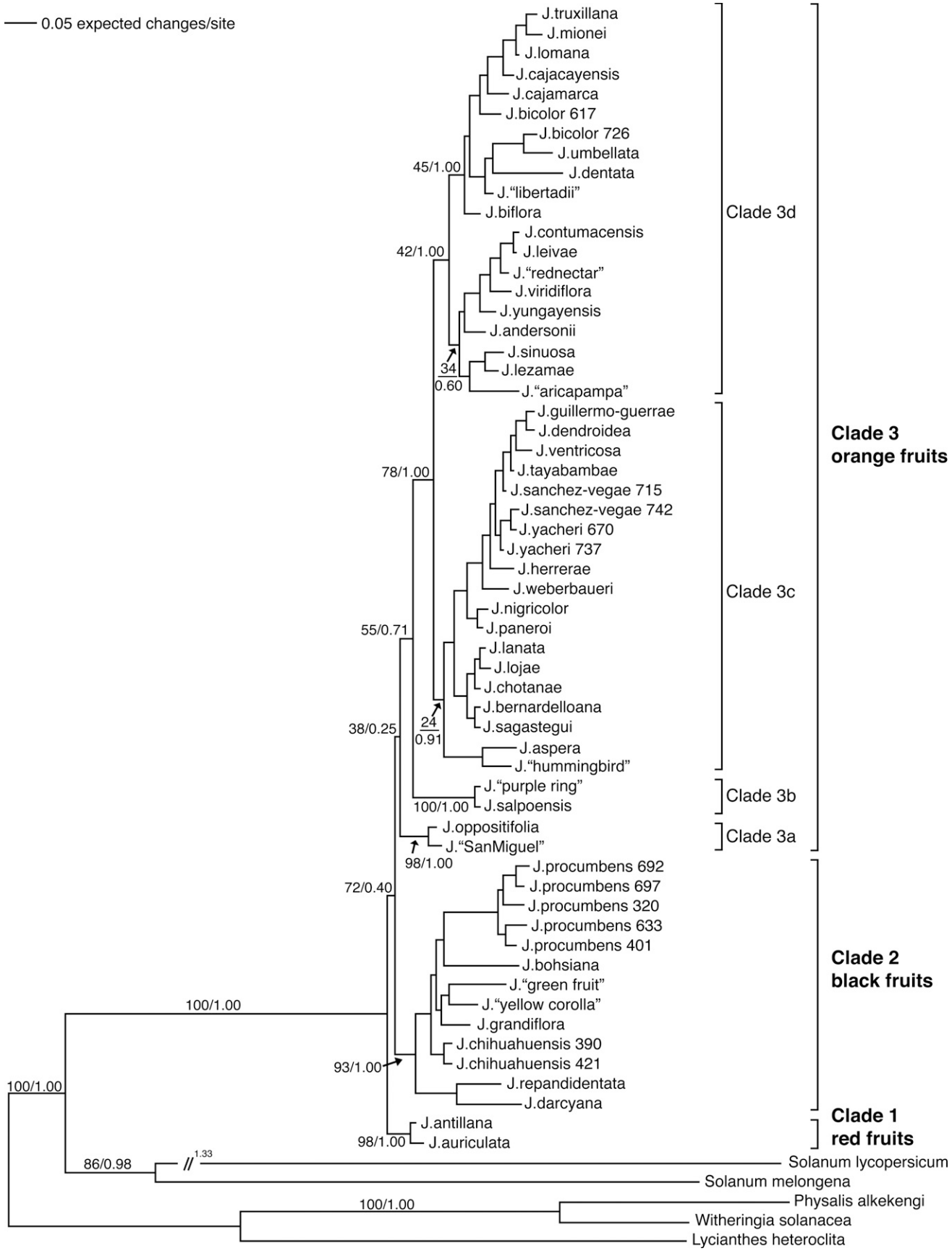
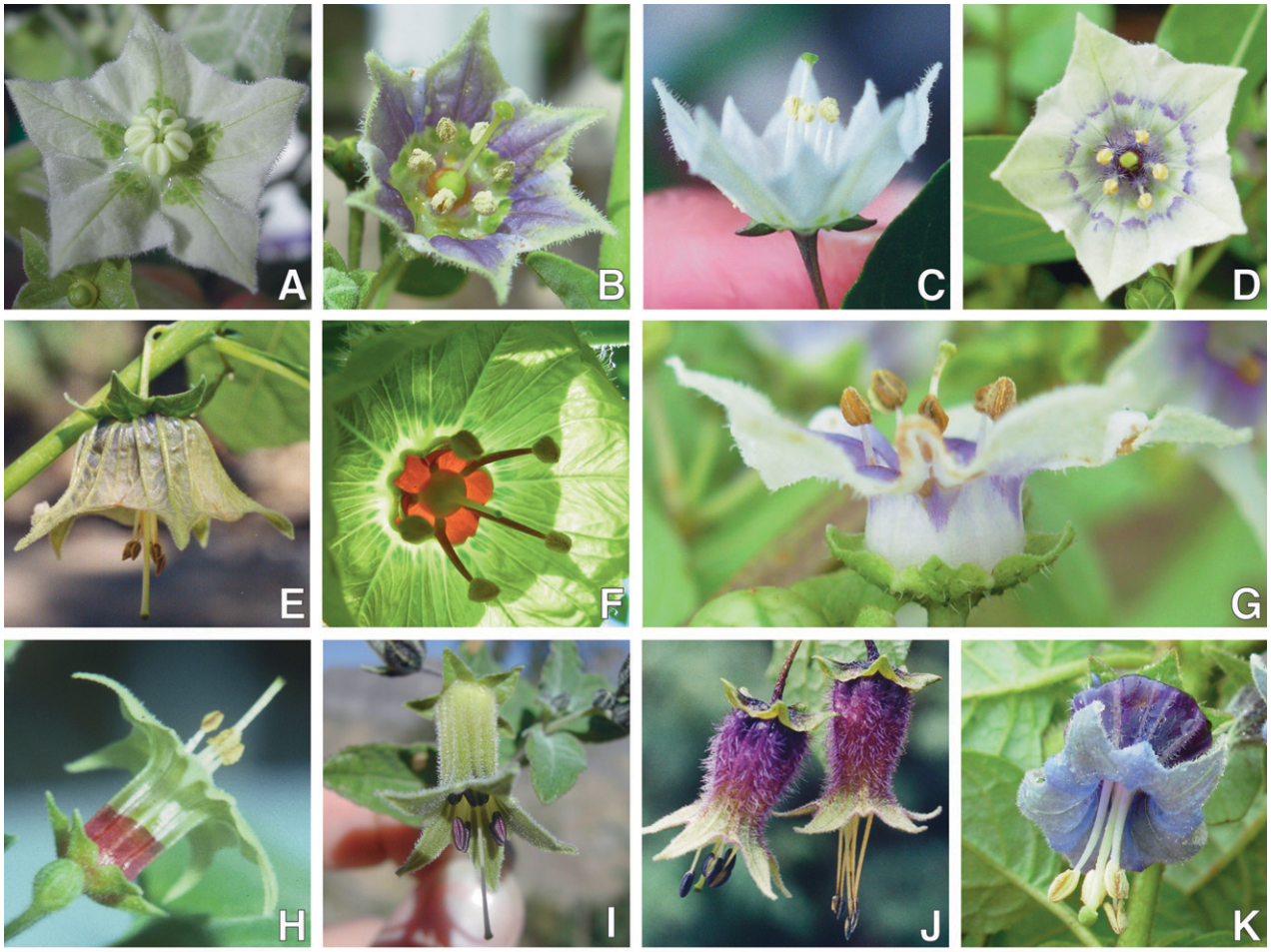


FIG. 2. Majority-rule consensus tree from MrBayes showing all compatible partitions and average branch lengths. Support values for early-diverging branches are included with ML bootstrap percentages first and posterior probabilities from Bayesian inference listed second. The branch length for an outgroup species, *Solanum lycopersicum*, was reduced, the actual length (1.33 expected changes/site) is reported next to the double hash mark on the branch.



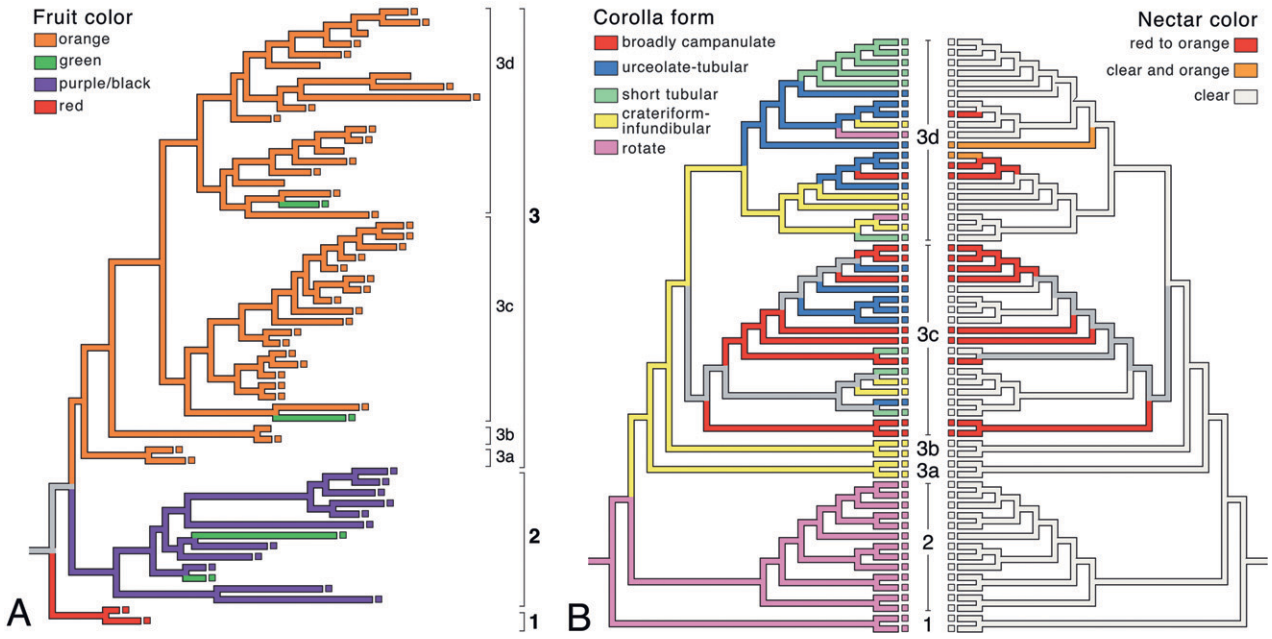


FIG. 3. Corolla diversity among *Jaltomata* species: a) rotate corolla of *J. grandiflora*; b-d) crateriform-infundibular corollas; b) *J. yungayensis*; c) *J. oppositifolia*; d) *J.* "purple ring"; e-f) broadly campanulate corollas; e) *J. tayabambae*; f) *J.* "hummingbird"; g) short tubular corolla of *J. cajamarca*; h-k) urceolate-tubular corollas; h) *J. umbellata* with a large volume of red nectar; i) *J. bicolor* (726); j) *J. bicolor* (617), photo by Segundo Leiva; k) *J. yacheri*. Except where indicated, photos by T. Mione. Ancestral character reconstructions: a) fruit color (parsimony step #: 6); b) corolla form (left side) and nectar color (right side) (parsimony step #: 18, 9). Reconstructed nodes showing equivocal states are shaded gray.

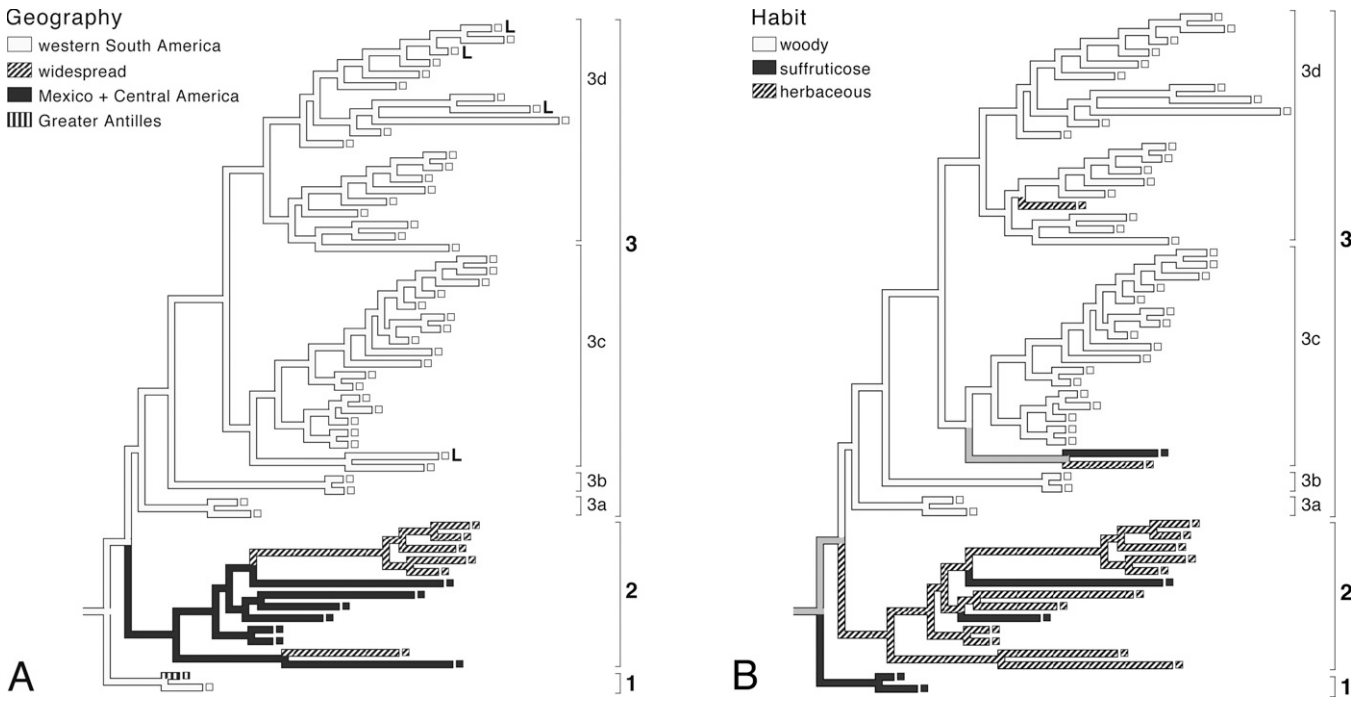


FIG. 4. Ancestral character reconstructions: a) geography, lomas species indicated with an 'L' (parsimony step #: 4); b) habit (parsimony step #: 7). Reconstructed nodes showing equivocal states are shaded gray.

red fruits (Fig. 4a), and a suffruticose habit where the plant is herbaceous except for a woody base (Fig. 5b). Support for this lineage as sister to the rest of *Jaltomata* is weak; the monophyly of the remaining species show moderate to low support in the two phylogenetic analyses (72 bs/0.40 PP). Based on cpDNA restriction site analysis, these two species have been grouped previously with other South American *Jaltomata* species producing orange fruits (clade 3) with strong support (Mione et al. 1994).

Clade 2—The nine species in clade 2 generally produce black/purple fruits (Fig. 4a) and bear pale-green, rotate corollas (Figs. 3a, 4b). These are primarily herbaceous plants, except for two suffructicose species, *Jaltomata bohsiana* and *J. grandiflora* (Fig. 5b). Species are narrowly distributed in Mexico and Central America except for two widespread species, *Jaltomata procumbens* and *J. repandidentata*, of southern North America, Central America, and western South America (Fig. 5a). *Jaltomata procumbens* is a morphologically variable species, whereas *J. repandidentata* is uniform in appearance throughout its range. Both species were sampled only in the northern portion of their range (Mexico and Central America) for this study. *Jaltomata procumbens* is genetically variable also, with five unique sequences among the six specimens sampled, and with sequence divergence comparable to many species groups elsewhere in *Jaltomata*, while *J. repandidentata* is genetically uniform for the five collections sampled (Table 2).

Clade 3—Species of clade 3 are generally orange-fruited (Fig. 4a), shrubby plants (Fig. 5b). Clade 3 has only weak support in the phylogenetic analysis, but is further supported by these shared traits. Predominately distributed in western South America (Fig. 5a), these species are morphologically diverse in corolla color and corolla form (Fig. 4b) and in nectar color (Fig. 4b). Four subclades are resolved in the *waxy* phylogeny, but the branching order has low support (Figs. 1–2). Species of both clades 3a and 3b bear flowers with crateriform to infundibular corollas (Figs. 3c–d,4b). Species of clades 3c and 3d vary in corolla shape and nectar color (Figs. 3b, 3e–k, 4b). Two species, *Jaltomata aspera* and *J.* "hummingbird," are sister to the remaining species of clade 3c and share a distinct stamen, style, and stigma morphology (Fig. 3f). In both species, the fusion of the staminal bases creates a distinct floral bowl where nectar pools, as opposed to pooling

TABLE 3. Gene comparisons between *Jaltomata sinuosa*, *J. procumbens*, and *Solanum lycopersicum* for *ndhF* (AF500835, U47429, U08921) and *trnT-trnF* (DQ180418, DQ180419, DQ180450) (Weese and Bohs 2007); *Jaltomata dentata* (EF438985), *J. hunzikeri* (EF438939), and *Solanum lycopersicum* (EF438904) (Hu and Saedler, 2007) were compared for *matK*. For *waxy*, *Solanum lycopersicum* (AP009280), *Jaltomata procumbens* (GU256344), and *J. sinuosa* (GU256305) from this study were compared.

		aligned sequence length	# sites different		uncorrected "p" distance	
gene	genome		*Jaltomata*	Solaneae	*Jaltomata*	Solaneae
ndhF	chl	2,086	4	39–43	0.00192	0.0187–0.0206
trnT-trnF	chl	1,972	10	47–53	0.005	0.0269–0.0304
matK	chl	932	2	24–26	0.00215	0.0258–0.279
waxy	nuc	2,598	29	175–180	0.01185	0.0765–0.0788

TABLE 4. Ancestral character state reconstruction performed using Mesquite's unordered parsimony model. A parsimony step represents a change from any one state to another.

Character	Parsimony Steps	Figure
fruit color	6	4a
corolla form	18	4b
nectar color	9	4b
geography	4	5a
habit	7	5b

on the corolla as in other *Jaltomata* species. The stigma is not capitate as in other species; these two species have a style that is broadest at the base and narrows distally.

Character Evolution—Corolla shape is labile, with each form appearing to have evolved multiple times. Rotate corollas are found in the earliest-diverging lineage in *Jaltomata* and in all but a few *Solanum* species (Nee 1999; Hunziker 2001; Bohs et al. 2007), suggesting it as the ancestral form in *Jaltomata* (Fig. 4b). The crateriform corolla (Figs. 3b-d) occurs in several species and is inferred to be the ancestral form for clade 3 (Fig. 4b). The various other corolla shapes may have evolved from crateriform corollas including two reversals back to rotate within clade 3d in *Jaltomata* "libertadii" and *J. sinuosa* (Fig. 4b). The data support the distinct floral bowl created from the fusion of staminal bases in *J. aspera* and *J.* "hummingbird" as a synapomorphy.

Jaltomata species producing red-colored nectar are not a monophyletic group (Fig. 4b). All *Jaltomata* species with broadly campanulate corollas produce red/orange nectar and a subset of the species with tubular-urceolate corollas do as well. A correlation between corolla shape and colored nectar may implicate convergence for these traits by pollinator preference. Red/orange nectar coloration appears to have evolved several times independently, possibly in conjunction with the evolution of campanulate corollas. If this is true, then red nectar color has been lost when corolla morphology has changed, except in some instances where urceolate-tubular corollas have evolved from campanulate corollas and red nectar persisted in descendants with urceolate or tubular corollas (Fig. 4b). Hummingbirds have been observed visiting *J.* "hummingbird" (T. Mione, pers. observ.); however, the pollination biology of *Jaltomata* species with colored nectar remains unstudied. Red pigment has been studied in nectar of *Nesocodon* (Campanulaceae), yet its significance and role in pollination remains unclear (Olesen et al. 1998).

If clade 1 is sister to other *Jaltomata* and if red or orange fruits represent quantitative variation in fruit color, as distinct from the purple/black fruits, then red/orange fruits appear to be ancestral in *Jaltomata*. Purple/black berries evolved once and characterize one major clade. Green berries evolved at least three times independently from within both orange- and black-fruited lineages (Fig. 4a). Since all *Jaltomata* fruits are green when immature, the retention of green color into maturity seems to represent a case of neoteny in fruit development. Berries that split open when ripe to reveal the mature seeds may have evolved twice within clade 3c (*Jaltomata chotanae* and *J. sanchez-vegae*, T. M. and S. Leiva G., field observations), but a lack of resolution between these lineages clouds this assessment (Fig. 1).

Variants of *Jaltomata bicolor* may represent distinct species. The two forms collected in different departments of Peru bear corollas that differ in shape and color and do not form a monophyletic group within clade 3d (Fig. 1). Collections from Ancash, Peru (726) have a green, nearly straight-tubular corolla (Fig. 3i), whereas collections from Lima, Peru (617) have a purple, tubular-urceolate corolla (Fig. 3j). Two accessions from the Department of Ancash were sampled and had identical sequences (Table 2).

Each clade exhibits a characteristic habit (Fig. 5b). The two species in clade 1 are both suffruticose; plants are generally herbaceous except for a portion of stem close to the ground. Clade 2 is generally herbaceous with only two suffruticose species. The orange-fruited lineages of clade 3 are woody except for three species, two of which are herbaceous and one is suffruticose. Thus, inference regarding ancestral habit is equivocal. Most of these species habits were confirmed in the field (T. Mione, pers. observ.), but an exposed woody caudex in the herbaceous species, *J.* "hummingbird" was observed in greenhouse-grown plants. This feature was not visible in the field but implies that species labeled as herbaceous may actually exhibit a suffruticose habit. If many herbaceous species are indeed suffruticose, the ancestral habit of *Jaltomata* would be inferred to be suffruticose.

Biogeography—*Jaltomata* species occur from Arizona, U. S. A., to Bolivia, on the Galapagos Islands, and in the Greater Antilles. *Solanum*, the sister group of *Jaltomata*, most likely originated in South America (Olmstead et al. 2008) and we infer that *Jaltomata* did as well (Fig. 5a). Except for the black/purple-fruited, primarily Mesoamerican clade, the remainder of the *Jaltomata* clades are restricted to South America (except for *J. antillana* in clade 1, which is morphologically and genetically similar to the South American *J. auriculata*).

The black/purple-fruited clade of *Jaltomata* is distributed predominantly in Mexico and Central America with a couple of widespread species that dispersed back to South America *(J. procumbens* and *J. repandidentata).* A black/purple-fruited ancestor may have originated in South America and then successfully colonized Mexico and Central America once (Fig. 5a). Although less species-rich and more morphologically uniform, the black/purple-fruited clade is more widely distributed than any other.

The *Jaltomata* species of the Peruvian lomas are not monophyletic. Three species of clade 3d, *Jaltomata lomana, J. truxillana* and *J. umbellata* are confined to lomas, while *J. aspera*, a species of the early diverging lineage of clade 3c, grows both in the lomas and in the Andes (the representative *J. aspera* plant from which DNA was extracted was from the Andes, not from the lomas). *Jaltomata truxillana* and *J. lomana* are closely related, but grow some 190 km away from each other on virtual islands. Given the phylogenetic distance among the lomas representatives, it seems unlikely that an ancestral lomas species diversified and colonized other lomas communities. Instead, colonization may have occurred a number of times by different Andean lineages. Whichever scenario is invoked, the ability to live in lomas has evolved more than once after multiple dispersal events from the Andes.

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Appendix 1. List of taxa investigated, organized as follows: taxon name and authority, collection locality, collector and voucher number, (herbarium acronym), GenBank accession number for *waxy*.

Jaltomata Schltdl. - *J. andersonii* Mione, Peru, Lima, *T. Mione et al. 616* (NY), GU256308; *J. antillana* (Krug and Urban) D'Arcy, Dominican Republic, La Vega, *T. Mione & F. Jimenez 547* (COLO), GU256357; *J.* "aricapampa", Peru, La Libertad, *T. Mione et al. 716* (CCSU), GU256307; *J. aspera* (R. & P.) Mione, Peru, Lima, *T. Mione et al. 615* (CCSU), GU256332; *J. auriculata* (Miers) Mione, Ecuador, Pichincha, *Plowman & Davis 4449* (GH), GU256358; *J. bernardelloana* S. Leiva & Mione, Peru, La Libertad, *T. Mione et al. 640* (CCSU), GU256330; *J. bicolor* (Ruiz López & Pavón) Mione, Peru, Lima, *T. Mione et al. 617* (CCSU), GU256301; *J. bicolor* (Ruiz López & Pavón) Mione, Peru, Ancash, *T. Mione et al. 726* (CCSU), GU256289; *J. bicolor* (Ruiz López & Pavón) Mione, Peru, Ancash, *T. Mione et al. 728* (CCSU), GU256290; *J. biflora* (R. & P.) Benítez, Peru, Junin, *D. Mugaburu 5 & 6* (CCSU), clone a: GU256302, clone b: GU256303; *J. bohsiana* Mione, Mexico, México, *D. M. Spooner & J. Gómez 4253* (MEXU), GU256349; *J. cajacayensis* S. Leiva & Mione, Peru, Ancash, *T. Mione et al. 729* (CCSU), GU256298; *J. cajamarca* Mione, Peru, Cajamarca, *A. Sagástegui A. 14389* (CONN), clone a: GU256299, clone b: GU256300; *J. chihuahuensis* (Bitter) Mione & Bye, Mexico, Chihuahua, *T. Davis 1180* (MO), GU256347; *J. chihuahuensis* (Bitter) Mione & Bye, Mexico, Chihuahua, *Mione 421* (CONN), GU256348; *J. chotanae* S. Leiva & Mione, Peru, Cajamarca, *T. Mione et al. 731* (HAO), GU256327; *J. contumacensis* S. Leiva & Mione, Peru, Cajamarca, *T. Mione et al. 656* (MO), GU256309; *J. darcyana* Mione, Costa Rica, Nicoya Peninsula, *T. Mione & L. Yacher 694* (CR), GU256356; *J. dendroidea* S. Leiva & Mione, Peru, La Libertad, *T. Mione et al. 719* (CCSU), GU256315; *J. dentata* (Ruiz & Pav.) Benítez, Peru, Lima, *T. Mione et al. 610* (CCSU), GU256293; *J. dentata* (Ruiz & Pav.) Benítez, Peru, Lima, *T. Mione et al. 618* (CCSU), GU256292; *J. grandiflora* (Robinson and Greenmann) D'Arcy, Mione & Davis, Mexico, Michoacan, *Davis 1114* (MO), GU256350; *J.* "green fruit," Mexico, Mexico D. F., *T. Mione 349* (CONN), GU256345; *J. guillermo-guerrae* Mione & S. Leiva, Peru, La Libertad, *T. Mione et al. 713* (CCSU), GU256314; *J. herrerae* (C. V. Morton) Mione, Bolivia, La Paz, *Mione et al. 564* (LPB), GU256321; *J.* "hummingbird", Peru, La Libertad, *Mione & Leiva 758* (CCSU), GU256333; *J. lanata* S. Leiva & Mione, Peru, Cajamarca, *T. Mione et al. 741* (CCSU), GU256328; *J. leivae* Mione, Peru, Cajamarca, *T. Mione et al. 660* (CCSU), GU256310; *J. lezamae* S. Leiva & Mione, Peru, Cajamarca, *M. O. Dillon et al. 6505 and/or 6508* (F), GU256306; *J.* "libertadii", Peru, La Libertad, *T. Mione et al. 650* (CCSU), GU256294; *J. lojae* Mione, Ecuador, Loja, *D. M. Spooner et al. 5037* (CONN), GU256329; *J. lomana* Mione & S. Leiva, Peru, Ancash, *Mione et al. 631* (NY), GU256297; *J. mionei* Leiva G. & Quipuscoa, Peru, La Libertad, *Mione et al. 637* (CCSU), GU256296; *J. nigricolor* S. Leiva & Mione, Peru, La Libertad, *T. Mione et al. 718* (F), GU256325; *J. oppositifolia* S. Leiva & Mione, Peru, Cajamarca, *Mione et al. 674* (F), GU256337; *J. paneroi* Mione & S. Leiva, Peru, Cajamarca, *Mione et al. 705* (CCSU), GU256326; *J. procumbens* (Cav.) J. L. Gentry, Mexico, Chiapas, *Mione 401* (CCSU), GU256344; *J. procumbens* (Cav.) J. L. Gentry, Guatemala, Quezaltenango, *D. Spooner et al. 7035* (BIGU), GU256342; *J. procumbens* (Cav.) J. L. Gentry, Mexico, Oaxaca, *D. Spooner et al. 959a* (CCSU), GU256343; *J. procumbens* (Cav.) J. L. Gentry, Costa Rica, *T. Mione & L. Yacher 692* (CCSU), GU256339; *J. procumbens* (Cav.) J. L. Gentry, Costa Rica, Alajuela, *T. Mione & L. Yacher 699* (CCSU), GU256341; *J. procumbens* (Cav.) J. L. Gentry, Costa Rica, *T. Mione & W. Haber 697* (CCSU), GU256340; *J.* "purple ring", Peru, Cajamarca, *Leiva et al. 3647* (CCSU), GU256334; *J.* "rednectar", Peru, Cajamarca, *T. Mione et al. 740* (CCSU), GU256311; *J. repandidentata* (Dunal) Hunz., Nicaragua, Granada, *T. Mione & F. Coe 555* (CONN), GU256351; *J. repandidentata* (Dunal) Hunz., Mexico, Veracruz, *Mione 571* (CONN), GU256352; *J. repandidentata* (Dunal) Hunz., Costa Rica, Puntarenas, *T. Mione & L. Coe 605* (CCSU), GU256353; *J. repandidentata* (Dunal) Hunz., Costa Rica, San Jose prov., *T. Mione & L. Yacher 691* (CCSU), GU256354; *J. repandidentata* (Dunal) Hunz., Costa Rica, Puntarenas, *T. Mione & W. Haber 696* (CCSU), GU256355; *J. sagastegui* Mione, Peru, Cajamarca, *T. Mione et al. 755* (CONN), GU256331; *J. salpoensis* S. Leiva G. & Mione, Peru, La Libertad, *T. Mione et al. 639* (CCSU), GU256336; *J. salpoensis* S. Leiva G. & Mione, Peru, Amazonas, *T. Mione et al. 706* (CCSU), GU256335; *J. sanchez-vegae* S. Leiva & Mione, Peru, La Libertad, *T. Mione et al. 647* (CCSU), GU256318; *J. sanchez-vegae* S. Leiva & Mione, Peru, La Libertad, *T. Mione et al. 715* (CCSU), GU256322; *J. sanchez-vegae* S. Leiva & Mione, Peru, Cajamarca, *T. Mione et al. 742* (CCSU), GU256319; *J.* "SanMiguel," Peru, Cajamarca, *T. Mione et al. 738* (CCSU), GU256338; *J. sinuosa* (Miers) Mione, Peru, Amazonas, *T. Mione et al. 708* (CCSU), GU256304; *J. sinuosa* (Miers) Mione, Peru, Cajamarca, *T. Mione et al. 733* (HAO), GU256305; *J. tayabambae* S. Leiva & Mione, Peru, La Libertad, *T. Mione et al. 722* (CCSU), GU256316; *J. truxillana* S. Leiva & Mione, Peru, La Libertad, *T. Mione & S. Leiva G. 759* (CCSU), GU256295; *J. umbellata* (Ruiz López & Pavón) Mione, Peru, Lima, *T. Mione & L Yacher 730* (CCSU), GU256291; *J. ventricosa* (Baker) Mione, Peru, La Libertad, *T. Mione et al. 712*, GU256317; *J. viridiflora* (Humb., Bonpl. & Kunth) M. Nee & Mione, Ecuador, Carchi, *T. Mione & S. McQueen 460* (HAO), GU256312; *J. weberbaueri* (Dammer) Mione, Peru, Ancash, *T. Mione et al. 725* (CCSU), GU256324; *J. yacheri* Mione & S. Leiva, Peru, Cajamarca, *T. Mione et al. 670* (CCSU), GU256320; *J. yacheri* Mione & S. Leiva, Peru, Cajamarca, *T. Mione et al. 737* (CCSU), GU256323; *J.* "yellow corolla", Mexico, Mexico D.F., *T. Mione & R. Bye 602* (CCSU), GU256346; *J. yungayensis* Mione & S. Leiva, Peru, Ancash, *T. Mione et al. 723* (CCSU), GU256313.