

## SYSTEMATIC IMPLICATIONS OF CHLOROPLAST DNA VARIATION IN *JALTOMATA* AND SELECTED PHYSALOID GENERA (SOLANACEAE)<sup>1</sup>

THOMAS MIONE,<sup>2</sup> RICHARD C. OLMSTEAD, ROBERT K. JANSEN, AND  
GREGORY J. ANDERSON

Biological Sciences, Central Connecticut State University, New Britain, Connecticut 06050-4010;  
Environmental, Population, and Organismal Biology, University of Colorado, Boulder, Colorado 80309-0334;  
Department of Botany, University of Texas, Austin, Texas 78713; and  
Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043

Chloroplast DNA restriction site data were used to assess relationships among the solanaceous genera *Jaltomata*, *Hebecladus*, Old and New World *Physalis*, *Chamaesaracha*, *Leucophysalis*, *Margaranthus*, *Nicandra*, and *Saracha*, and to assess interspecific relationships within *Jaltomata*. Cladograms rooted with *Nicotiana tabacum* were constructed with Wagner and Dollo parsimony. Strict consensus trees indicate that *Hebecladus* originated from within *Jaltomata*; together these genera are monophyletic and constitute the recently circumscribed genus *Jaltomata*. There are two primary clades in *Jaltomata*: one a morphologically diverse group confined to western (largely Andean) South America, the Greater Antilles, and the Galápagos Islands; and the other a morphologically homogeneous group widely distributed from the southwestern United States to Bolivia. The controversial *Leucophysalis viscosa*, formerly treated as *Jaltomata viscosa*, is related to *Leucophysalis*, *Physalis*, *Chamaesaracha*, and *Margaranthus*; it does not group with any of the sampled species of *Jaltomata*. *Physalis* appears to be polyphyletic since *P. alkekengi* of the Old World branches off prior to a clade including *Chamaesaracha*, *Margaranthus*, and the two New World *Physalis* species sampled.

*Jaltomata* (including *Hebecladus*) (tribe Solaneae, subfamily Solanoideae) contains about 30 herbaceous to shrubby species, distributed from the southwest United States to southern Bolivia, with one species each on the Galápagos Islands and in the Greater Antilles (Mione, Anderson, and Nee, 1993). There are two regions of relatively high species diversity: western South America north of Argentina with about 20 species, and Mexico with about ten species. In a chloroplast DNA (cpDNA)-based generic study of the Solanaceae, Olmstead and Palmer (1992) found that *Jaltomata* is probably the sister group of the clade comprised of *Solanum* (e.g., potatoes), *Lycopersicon* (tomatoes), and *Cyphomandra* (tree tomatoes). The fruits and root-stocks of both wild and semidomesticated *Jaltomata* species are consumed by humans (Davis and Bye, 1982; Williams, 1985; Laferrière, Weber, and Kohlhepp, 1991; Mione, 1992; Mione, Anderson, and Nee, 1993).

*Jaltomata* and *Hebecladus* had been distinguished largely on the basis of the rotate to broadly campanulate corolla and herbaceous habit of *Jaltomata* (Davis, 1980), in contrast to the tubular to infundibular corolla and

shrubby habit of *Hebecladus* (Miers, 1845). Hunziker (1979) and Nee (1986), recognizing that these genera grade into one another, suggested that these should be treated as a single genus, *Jaltomata*. Yet some contemporary workers (Davis, 1980; D'Arcy, 1986) retained these as separate genera. Thus, a study of molecular characters was conducted to help resolve this issue, and to complement continuing morphological and biogeographic studies (Knapp, Mione, and Sagástegui, 1991; D'Arcy, Mione, and Davis, 1992; Mione, 1992; Mione and Coe, 1992; Mione, Anderson, and Nee, 1993).

Treatment of *Leucophysalis viscosa* (Schrader) A. T. Hunz. has been controversial. It has been variously treated in six different genera, recently as *Jaltomata viscosa* (Schrader) D'Arcy & Davis (Gentry, 1972; Hunziker, 1991). Hunziker (1961) and M. Nee of the New York Botanical Garden (personal communication) suggested that this species may be more closely related to *Physalis* than to *Jaltomata*. During the course of this study the species was transferred to *Leucophysalis* by Hunziker (1991), based on morphological and anatomical investigations of flowers, fruits, and seeds. This species had also been treated as *Saracha viscosa* Schrader and *Physalis schraderiana* (Schrader) Bernhardt (Hunziker, 1961, 1991; Gentry, 1972).

The only hypothesis of relationships proposed within what now constitutes *Jaltomata* is that of Bitter (1921, 1924). Bitter retained *Hebecladus* as a distinct genus and divided *Jaltomata* (as *Saracha*) into five sections. Four of five sections of *Saracha* erected seem highly artificial, but sect. *Macrosaracha*, which includes species of Peru and Bolivia with campanulate corollas, may be a monophyletic group (Morton, 1938; Mione, 1992).

Our primary objectives were to: 1) assess with cpDNA evidence the circumscriptions of *Jaltomata* suggested by recent workers; 2) provide evidence to be used in the

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<sup>2</sup> Author for correspondence.

proper placement of "*Jaltomata viscosa*"; and 3) assess interspecific relationships within *Jaltomata*, discussing morphology and biogeography in light of our results. The genera included in this study (see below), although not constituting a monophyletic group in the generic study of Olmstead and Palmer (1992), were chosen to best address these objectives. Two genera in which *L. viscosa* has been treated (*Athenaea*, *Witheringia*) were not included in this study because we consider these inappropriate based on morphological evidence.

## MATERIALS AND METHODS

Fourteen species of *Jaltomata* (including *Hebecladus*) and one to three species each of *Chamaesaracha*, *Leucophysalis*, *Margaranthus*, *Nicandra*, *Physalis*, *Saracha*, and *Nicotiana* were used (Table 1). Species yet to be transferred from another genus into *Jaltomata* are listed in Table 1 in the genus in which they are currently recognized, but are discussed and represented in the figures as *Jaltomata* species.

The restriction enzymes used were as in Olmstead and Palmer (1992) with the addition of BstN I, Dra I, Hae III, Hinc II, and Rsa I. A total of 11, six-base-pair restriction enzymes and four, four-base-pair restriction enzymes was used. All restriction fragments were mapped as described in Olmstead and Palmer (1992). For each enzyme the position of restriction sites (and therefore the size of fragments) resulting from digestion of the *Nicotiana tabacum* genome was known from computer searches of the complete tobacco cpDNA sequence (Shinozaki et al., 1986) on GENBANK. This usually allowed the size of fragments to be determined with great accuracy. Length mutations were not used in the phylogenetic analyses.

The computer package PAUP (version 3.1.1; Swofford, 1991) was used for cladistic analyses. Autapomorphies were not included in the data matrix but were added to the tree after computer analysis. We chose the outgroups *Nicotiana tabacum* and *Nicandra physaloides* based on the results of Olmstead and Palmer (1992). Although these two genera were not the closest outgroup in Olmstead and Palmer's (1992) study, they are clearly related to and outside of the ingroup genera included in our analysis. Restriction sites that were variable in the two outgroups were eliminated because of the uncertainty about character polarity, yet this approach generated the same strict consensus tree topology as trees generated using only *N. tabacum* as an outgroup. Thus, only *N. tabacum* was used as an outgroup in subsequent analyses, and *Nicandra* was considered a member of the ingroup. Wagner and Dollo analyses used the Tree Bisection Reconnection (TBR) and Mulpars options. One hundred random entries of the data were performed in an attempt to locate all equally parsimonious trees (Maddison, 1991). Bootstrap analyses were conducted with 100 replications and the TBR option (without Mulpars) to provide a measure of support for the monophyletic groups identified in the Wagner and Dollo analyses.

## RESULTS

One hundred and eight phylogenetically informative characters were used in parsimony analyses (data matrix

TABLE 1. Abbreviations, authorities, and voucher information. Names given in quotations represent either unpublished species or species yet to be transferred to *Jaltomata*.

Jaltomata procumbens1, <i>Jaltomata procumbens</i> (Cav.) J. L. Gentry—MEXICO: <i>T. Davis IV 1189</i> Tlaxcala, CONN; <i>T. Davis IV 1191</i> Mexico, CONN; <i>R. Torres C. 3765</i> Chihuahua, MO.
Jaltomata procumbens2, <i>Jaltomata procumbens</i> (Cav.) J. L. Gentry—MEXICO, Chihuahua: <i>R. Bye 10084</i> , COLO; <i>T. Davis IV 1130</i> , CONN.
Jaltomata green fruited, <i>Jaltomata procumbens</i> (Cav.) J. L. Gentry—MEXICO, Tlaxcala: <i>D. E. Williams s.n.</i> , CONN, probably CHA-PA.
<i>Jaltomata grandiflora</i> (Robinson & Greenm.) D'Arcy, Mione & Davis—MEXICO, Michoacan: <i>T. Davis IV 1114</i> , CONN.
" <i>Jaltomata chihuahuaensis</i> ," <i>Saracha chihuahuaensis</i> Bitter—MEXICO, Chihuahua: <i>R. Bye 14243</i> , COLO [fruit green]; <i>T. Davis IV 1180</i> [fruit purple], CONN.
<i>Jaltomata repandidentata</i> (Dunal) A. T. Hunz.—MEXICO, Guerrero: <i>T. Davis IV 822</i> , CONN.
" <i>Jaltomata conspersa</i> ," <i>Saracha conspersa</i> Miers—MEXICO: <i>R. Bye 10219</i> Morelos, CONN, MEXU; <i>D. Spooner 4253</i> Mexico, CONN.
" <i>Jaltomata oaxaca</i> " (Mione, unpublished data)—MEXICO, Oaxaca: <i>D. Spooner 4173</i> , CONN.
<i>Jaltomata glandulosa</i> Castillo & R. E. Schultes—ECUADOR, Chimborazo: <i>T. Mione &amp; C. McQueen 468/469</i> , COLO, CONN.
" <i>Jaltomata paneroi</i> " (Mione, unpublished data)—PERU, Cajamarca: <i>J. Panero 854</i> , CONN.
" <i>Jaltomata auriculata</i> ," <i>Saracha auriculata</i> Miers—ECUADOR, Pichincha: <i>T. Plowman 4449</i> , CONN, GH, K [same accession/DNA sample used in Olmstead and Palmer (1992) as <i>J. dentata</i> ].
<i>Jaltomata ventricosa</i> (Baker) Mione—PERU, Cajamarca: <i>S. Leiva 138</i> , CONN, F but not seen [formerly <i>Hebecladus</i> ].
" <i>Jaltomata sagastegui</i> " (Mione, unpublished data)—PERU, Cajamarca: <i>A. Sagastegui A. 14388</i> , CONN, F but not seen.
" <i>Jaltomata cajamarca</i> " (Mione, unpublished data)—PERU, Cajamarca: <i>A. Sagastegui A. 14389</i> , CONN, F but not seen.
<i>Jaltomata viridiflora</i> (H.B.K.) M. Nee & Mione—Ecuador, Carchi: <i>T. Mione &amp; C. McQueen 460</i> , CONN [formerly <i>Hebecladus</i> ].
<i>Jaltomata antillana</i> (Krug & Urban) D'Arcy—Dominican Republic, La Vega: <i>T. Mione &amp; F. Jimenez 547</i> , COLO, CONN, USD.
<i>Saracha punctata</i> R. & P.—PERU, Cochabamba: <i>R. Guillén U. 18</i> , CONN [det. by A. T. Hunziker].
<i>Saracha spinosa</i> (Dammer) W. G. D'Arcy & D. N. Smith — <sup>a</sup>
<i>Physalis peruviana</i> Mill—Jardín Botánico de Bogotá, Colombia, R. G. Olmstead s.n., COLO.
<i>Physalis heterophylla</i> Nees—U.S.A., Michigan: <i>R. G. Olmstead 88-9</i> , COLO.
<i>Physalis alkekengi</i> L. — <sup>a</sup>
<i>Leucophysalis grandiflora</i> (Hook.) Rydb.—U.S.A., Michigan: <i>R. G. Olmstead 88-17</i> , COLO.
<i>Leucophysalis viscosa</i> (Schrader) A. T. Hunz.—MEXICO, Oaxaca: <i>R. Torres C. et al. 7108</i> , COLO, CONN, NY.
<i>Margaranthus solanaceus</i> Schldl. — <sup>a</sup>
<i>Chamaesaracha coronopus</i> (Dunal) Gray — <sup>a</sup>
<i>Nicandra physaloides</i> Gaertn. — <sup>a</sup>
<i>Nicotiana tabacum</i> L. — <sup>a</sup>

<sup>a</sup> See Olmstead and Palmer (1992) for collection/voucher information.

available on request from TM). Wagner analyses found 255 equally parsimonious trees with 132 steps (186 steps including autapomorphies) and a consistency index (CI) of 0.803 (excluding uninformative characters). Dollo parsimony found 196 equally parsimonious trees that were 136 steps long with a CI of 0.778 (excluding uninformative characters). Wagner and Dollo strict consensus trees had an identical topology (Fig. 1). One of the 255 Wagner trees is shown (Fig. 2) to illustrate the number of restriction site gains and losses supporting each node on a representative tree.

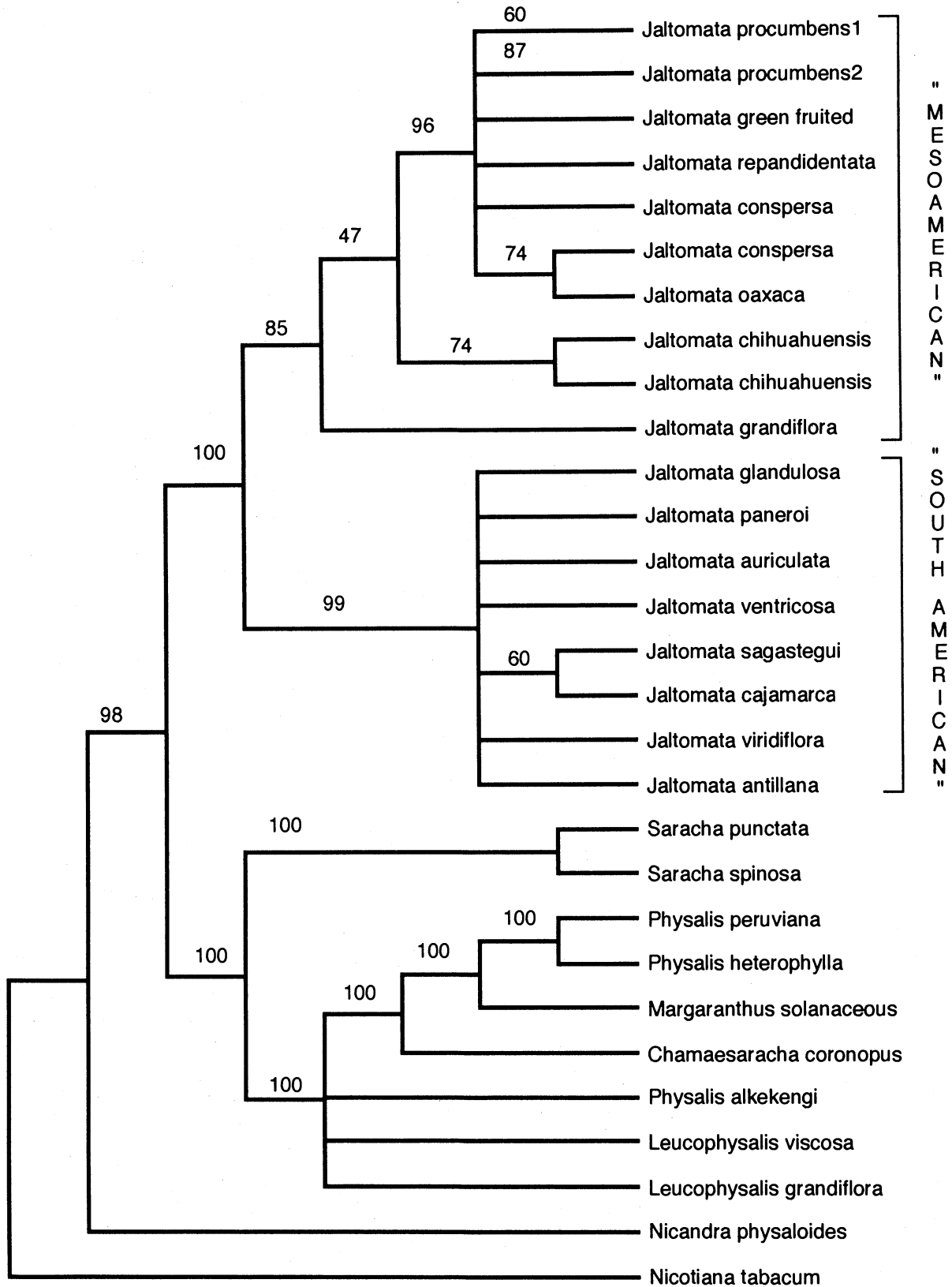


Fig. 1. Strict consensus of 255 equally most-parsimonious Wagner trees generated from chloroplast DNA restriction site mutations (length = 186; CI = 0.803 excluding autapomorphies). The percentage of Wagner bootstrap replicates supporting each clade is indicated along the internode for that clade. "Jaltomata procumbens1" and "Jaltomata procumbens2" show bootstrap values because more than one accession was used for each.

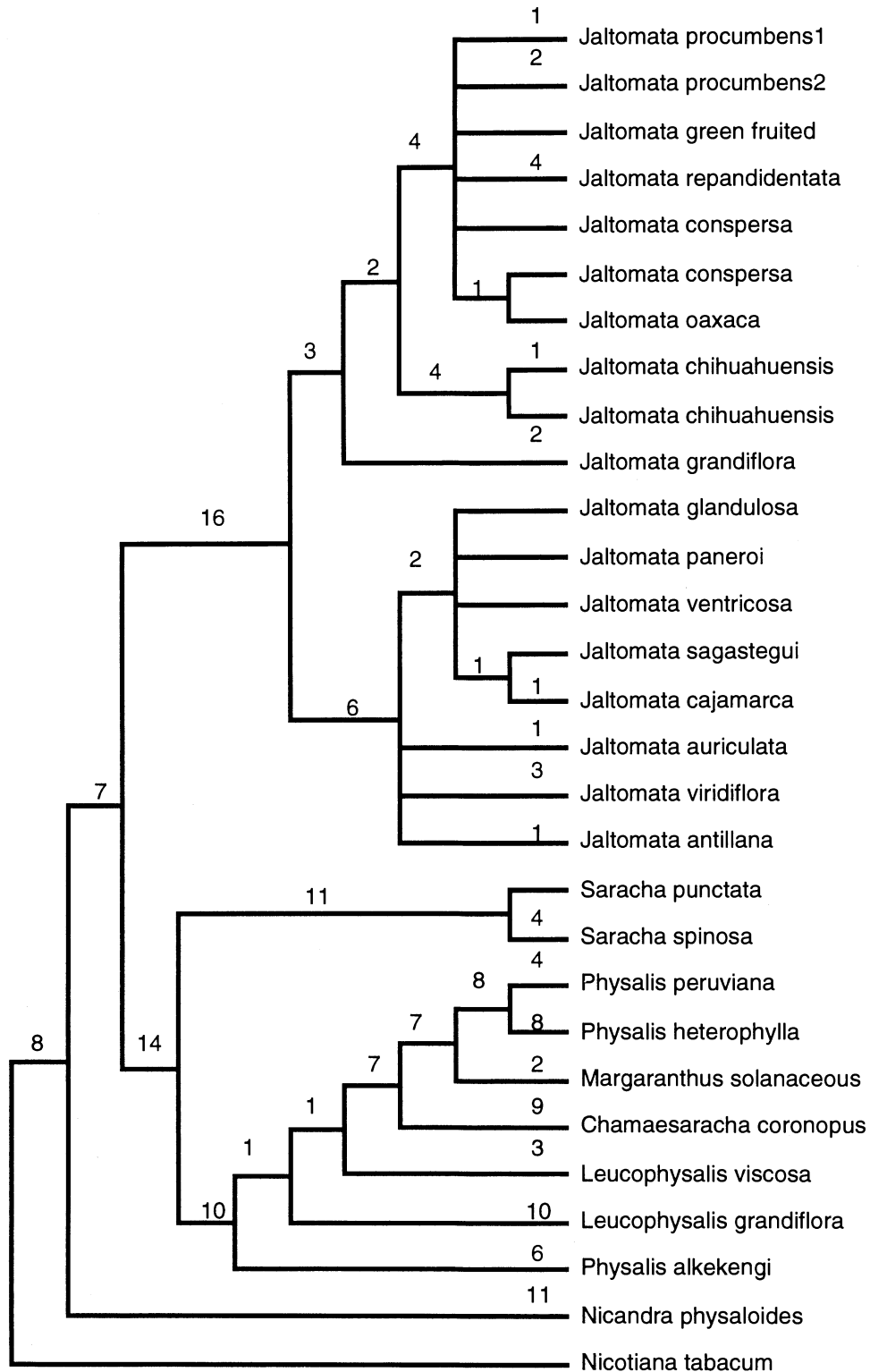


Fig. 2. One of the 255 equally parsimonious Wagner trees based on chloroplast DNA restriction site mutations (108 phylogenetically informative characters; length = 186; CI = 0.803 excluding autapomorphies). The number of restriction site mutations supporting each clade is indicated. The number of autapomorphies given is the sum of the autapomorphies that were not included in the data matrix and the number of homoplasies implied by the analysis. The two autapomorphies for “Jaltomata procumbens2” are actually synapomorphies for the two accessions representing “Jaltomata procumbens2.” The indicated autapomorphy for “Jaltomata procumbens1” is actually a synapomorphy for the three accessions representing “Jaltomata procumbens1.”

*Jaltomata*, as recently circumscribed to include *Hebecladus* species (Mione, Anderson, and Nee, 1993), is strongly supported as a monophyletic group (16 to 17 synapomorphies and a 100% bootstrap value). Numerous mutations also separate *Saracha* and *Jaltomata*.

The cpDNA phylogenies indicate that, given the sampling of genera here, *Nicandra* is the sister taxon to all other ingroup taxa, and that *Saracha* is the sister group of a clade including *Chamaesaracha*, *Leucophysalis*, *Margaranthus*, and *Physalis*. *Physalis* appears polyphyletic, with the Old World *P. alkekengi* branching off prior to the clade that includes the New World taxa *Chamaesaracha*, *Margaranthus*, *P. peruviana*, and *P. heterophylla*.

*Leucophysalis viscosa* (recently treated as *Jaltomata viscosa*, see above) does not group with *Jaltomata* (Figs. 1, 2). The cpDNA data provide strong support (14 synapomorphies and a 100% bootstrap value) that this species is allied with *Chamaesaracha*, *Leucophysalis*, *Margaranthus*, and *Physalis*.

Our cladograms reveal two principal clades in *Jaltomata*; based on their general phylogeography we refer to these as the "Mesoamerican" clade and the "South American" clade (Fig. 1). *Jaltomata grandiflora* is both the basal branch and the most morphologically distinct species of the "Mesoamerican" clade. The next to most basal branch of this clade, *J. chihuahuensis*, is represented by two accessions that differ in mature fruit color (Table 1; Mione, 1992). The remaining species of this clade are poorly resolved. However, two accessions of *J. procumbens* (having no detected differences in cpDNA, and therefore represented together as "J. procumbens2" in Figs. 1, 2) share a site loss, a site gain, and a small (approximately 0.1 kb) insertion. In addition, *J. oaxaca* and one accession of *J. conspersa* (*D. Spooner 4253*) share a site loss. The species of the "South American" clade are not resolved except for *J. sagastegui* and *J. cajamarca* from Peru (both Dpto. Cajamarca, Prov. Contumaza) that share a single restriction site gain.

## DISCUSSION

*Jaltomata* species were treated under *Saracha* (and *Hebecladus*, see below) until Gentry (1973, 1974) resurrected *Jaltomata* and set the stage for the removal from *Saracha* of the species appropriately placed in *Jaltomata*. As Davis (1980), Knapp, Mione, and Sagástegui (1991), and D'Arcy, Mione, and Davis (1992) have reiterated, *Jaltomata* and *Saracha* are distinguished by numerous morphological characters. Our cpDNA restriction site data also provide strong support for the distinction between *Saracha* and *Jaltomata*.

According to the restriction site data, *Jaltomata* would be paraphyletic without the inclusion of *Hebecladus*. *Jaltomata viridiflora* and *J. ventricosa* have been assigned to *Hebecladus*, yet these are clearly nested within the "South American" clade of *Jaltomata* (Figs. 1, 2). Thus, it is apparent that if these two species were treated as members of *Hebecladus*, the results would indicate that *Hebecladus* evolved from within *Jaltomata*. For the most part, the cpDNA tree lacks resolution within the "South American" clade, and therefore does not suggest a particular alignment of the species formerly attributed to *Hebecladus*.

Based on our cpDNA results, one possible approach would be to treat the "Mesoamerican" clade as *Jaltomata*, and within the "South American" clade retain *Hebecladus* and erect a third genus for the remainder of the species. However, there is a morphological continuum among all these species as recognized by Bitter (1924), Macbride (1962), Hunziker (1979), Nee (1986, personal communication), and Mione (1992), all of whom implied or suggested that *Jaltomata* and *Hebecladus* should be merged. Based on both the absence of morphological "gaps" between groups of species, and our cpDNA results, Mione, Anderson, and Nee (1993) unified *Jaltomata* and *Hebecladus*. Accordingly, all *Hebecladus* species have been or will be transferred to *Jaltomata* (e.g., Mione and Coe, 1992; Mione, Anderson, and Nee, 1993).

The basal placement of *Nicandra* and the sister group relationship of *Chamaesaracha*, *Margaranthus*, and *Physalis* to *Saracha* are in agreement with the results of the generic study of Olmstead and Palmer (1992). The close relationship of *Leucophysalis* to *Chamaesaracha*, *Margaranthus*, and *Physalis* is concordant with morphological studies of Averett (1973). The sister group relationship of *Jaltomata* to *Saracha*, *Chamaesaracha*, *Leucophysalis*, *Margaranthus*, and *Physalis* is almost certainly an artifact of our incomplete sampling of the tribe Solaneae. As stated, Olmstead and Palmer (1992) found that the clade made up of *Solanum* (e.g., potatoes), *Lycopersicon* (tomatoes), and *Cyphomandra* (tree tomatoes) is probably the sister group to *Jaltomata*. Thus, it is also highly likely that the morphological similarity of some species of *Jaltomata* to species of some physaloid genera is due to plesiomorphic characters (e.g., corolla maculae, longitudinal anther dehiscence, accrescent calyx, and self-compatibility).

Our understanding of the biosystematics of the physaloid genera was greatly improved by Averett (1973, with a key; 1979). He (1973) suggested that *Chamaesaracha* is probably most closely related to *Leucophysalis*. However, our results suggest that *Chamaesaracha* is most closely related to a clade including *Margaranthus* and the two New World species of *Physalis*. Averett (1979) also suggested that *Leucophysalis* and *Margaranthus* are probably closer to *Physalis* than is *Chamaesaracha*. Our results agree with this assertion with respect to *Margaranthus* and the New World species of *Physalis*, but disagree about the affinity of *Leucophysalis* to *Physalis* (Fig. 1).

*Leucophysalis viscosa* has been variously treated in six different genera (Hunziker, 1991). The cpDNA cladograms (Figs. 1, 2) provide equal support for placement of this problematic species in either *Leucophysalis* or in the clade of *Physalis* that includes *P. alkekengi*. The data do not support placement of *L. viscosa* in either *Saracha* or *Jaltomata* in which it has been placed. The proper placement of *L. viscosa* leads to a better understanding of phenotypic evolution in the tribe Solaneae. Specifically, *L. viscosa*, a species of the southern half of Mexico (possibly extending into Guatemala), lacks some characteristics of *Jaltomata* (basal pedicel articulation and oblique ventral filament insertion in bud), but it does share a few characters with some Andean *Jaltomata* species (viscous-gland-tipped hairs, lack of pubescence on the adaxial corolla face, and orange/red fruits). Because this species was

clearly positioned outside of *Jaltomata* in the cpDNA phylogeny, we conclude that morphological characters shared with some Andean *Jaltomata* have either evolved independently or are plesiomorphic and have been lost in other *Jaltomata* lineages.

Our results reveal sister clades in *Jaltomata*: a “Mesoamerican” clade and a “South American” clade (Fig. 1). In addition to the general geographic distribution of species, fruit color and habit are largely concordant with this result. The species of the “South American” clade are all South American with the exception of *J. antillana* of the Greater Antilles (*J. werffii* of the Galápagos Islands appears to be a member of this clade based on morphology, but was not included in this study because living material was not available). These are suffrutescent or shrubs, corollas are rotate, campanulate, or tubular, and fruits are red or orange.

The species of the “Mesoamerican” clade are distributed primarily in Mexico and Central America. A minor exception is *J. procumbens*, extending into southeastern Arizona, and a major range difference is manifest for *J. repandidentata*, which is distributed from Mexico to Bolivia (Polsgrove, Mione, and Anderson, 1993). The species of this clade are herbs with rotate corollas and purple/black fruits (two species include green-fruited races). In this clade only the basal species, *J. grandiflora*, is easily distinguished morphologically (D’Arcy, Mione, and Davis, 1992). In contrast, the six other species studied to date are difficult to distinguish morphologically when studied solely as dried specimens. *Jaltomata grandiflora* is the only species of this clade to share certain features with the “South American” clade: gland-tipped hairs on vegetative parts, a corolla greater than 3 cm in diameter, and more than 175 ovules per ovary are characters that are shared with a few species of the “South American” clade (Mione, 1992). However, because phylogenetic relationships within the “South American” clade are largely unresolved we cannot determine whether these shared features evolved in parallel or are plesiomorphic.

The “Mesoamerican” clade of *Jaltomata* includes several partially domesticated taxa (e.g., *J. chihuahuensis* and *J. procumbens*), utilized primarily for fresh fruit and starchy root-stocks (Davis and Bye, 1982; Williams, 1985; Davis, 1986; Mione, 1992). A semidomesticated form (“J. green fruited” in Figs. 1, 2) primarily of Tlaxcala, Mexico, having relatively large, green fruits (Williams, 1985), has been tentatively assigned to *J. procumbens* but may later be recognized as a distinct species (Mione, unpublished data). The more common purple/black fruited representatives of *J. procumbens* fall into two distinct cpDNA haplotypes, with one of the haplotypes (“J. procumbens2”) being represented by the two accessions from Chihuahua, Mexico. These two haplotypes also can be distinguished with a single morphological character: in the common garden and greenhouse, undehisced anthers of the accessions of “J. procumbens2” are less than 2 mm long, whereas undehisced anthers of the accessions of “J. procumbens1” are longer than 2 mm. Thus haplotype, anther size, and distribution congruently divide purple/black fruited *J. procumbens* into two distinct groups that may merit recognition as subspecies (subject to continuing study by TM).

The species of the “South American” clade included in this study span a markedly broader range of morphological variation than is present among members of the “Mesoamerican” clade. These species of the “South American” clade are suffrutescent and exhibit diverse corolla forms (e.g., rotate, campanulate, tubular, tubular with a rotate limb, tubular with a reflexed limb, and urceolate with a reflexed limb). Among these species there are also diverse corolla colors (e.g., purple, blue, green, pale-yellow, and white). Furthermore, nectar may be blood-red to orange and copious, or clear and present in small amounts, and corollas may or may not close at dusk, depending on the species (Mione, unpublished data). In contrast, members of the “Mesoamerican” clade are herbs with rather uniform corolla shape and color (corollas are rotate and either pale-green, pale-yellow, or pale-white). They produce small amounts of clear nectar, and the corollas close at dusk (Mione, unpublished data). Thus, the high degree of morphological differentiation present in the “South American” clade and the lack of cpDNA phylogenetic resolution suggest that rapid morphological evolution has given rise to the remarkable diversity present in this clade.

The two most basal species of the “Mesoamerican” clade (*J. grandiflora* and *J. chihuahuensis*) come from Michoacan (Central) and Chihuahua (Northern), Mexico, respectively. Consequently, the assertion that *Jaltomata* invaded Central and Northern Mexico by “. . . step-by-step local migration from the south” (D’Arcy, 1991) is not supported. Because the two sister groups are by definition of equal age, a region of origin for the genus cannot be determined. Regardless of the area in which the genus arose, dispersal to the secondary center, followed by establishment there, must have taken place early in the evolution of *Jaltomata*. In contrast, in another Latin American group (the *Aphelandra pulcherrima* complex) the morphology-based cladogram suggests that the invasion of Central America from South America has taken place several times (McDade, 1992).

Chloroplast DNA restriction site data provide new insights into generic relationships in Solaneae (a tribe that includes many economically important plants), and interspecific relationships in *Jaltomata*. Earlier workers treated *Jaltomata* (corollas rotate) and *Hebecladus* (corollas more or less tubular) as distinct genera, with the members of each genus being more similar to each other than to species of the other genus. We found these generic limits to be incongruent with our cpDNA phylogeny. The new circumscription of *Jaltomata*, based in part on our cpDNA results, removes the traditional generic boundary; *Jaltomata* and *Hebecladus* have been unified. *Jaltomata* includes two phylogenetic subgroups: the “Mesoamerican” clade includes most of the species traditionally treated as *Jaltomata*, and the “South American” clade includes the remainder of the traditional *Jaltomata* (e.g., *J. antillana*) and all ‘*Hebecladus*’ species. Thus, a few of the members of the “South American” clade are more similar morphologically to the members of the “Mesoamerican” clade than to members of their own clade. Although a departure from tradition, this new information and new generic delimitation markedly improve our understanding of biogeography. For example, instead of *J. antillana*

tacitly being assumed to be closely related to the other traditional *Jaltomata* (chiefly of Mexico and Central America), we now know that despite its rotate corolla, *J. antillana* of the Greater Antilles is closely related to Andean *Jaltomata*.

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