

A Festschrift for
**William
G. D'Arcy**

The Legacy of a Taxonomist

Edited by

Richard C. Keating

Victoria C. Hollowell

and

Thomas B. Croat



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A Festschrift for William G. D'Arcy

The Legacy of a Taxonomist

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Continued

JALTOMATA (SOLANACEAE) OF COSTA RICA

Thomas Mione and Leon Yacher

ABSTRACT. Three species of *Jaltomata* (Solanaceae) are recognized based on comparative morphology, including principal components analysis of morphological characteristics. *Jaltomata procumbens* grows from 1000 to 2900 m in Costa Rica and is distinguished by its straight filaments, anthers of uniform size, and straight styles. *Jaltomata repandidentata* grows from 400 to 1200 m, is characterized by its sigmoid filaments, anther size variation within the flower, and curved styles, and is reported from Central America for the first time. *Jaltomata darcyana* is a new species of the seasonally dry Pacific Coast, found from 0 to 320 m; it has straight filaments, anther size variation within the flower, and curved styles. The former two species are protogynous: anther dehiscence occurs the day after the flower opens. *Jaltomata darcyana*, however, lacks a pistillate phase and is functionally hermaphroditic when the flower opens. The first chromosome count for *J. darcyana* is reported: $2n = 24$. A key to the *Jaltomata* of Costa Rica is included.

RESUMEN. Tres especies de *Jaltomata* (Solanaceae) son reconocidas basándose en morfología comparada, incluyendo análisis de componentes principales (PCA) de caracteres morfológicos. *Jaltomata procumbens* es una especie que crece comúnmente entre los 1000–2900 m en Costa Rica y se distingue por presentar filamentos rectos, anteras de tamaño uniforme y estilos rectos. *Jaltomata repandidentata* es una especie que crece comúnmente entre los 400–1200 m; se caracteriza por tener filamentos sigmoides, anteras de tamaño variable dentro de la misma flor, estilos curvados, y se reporta por la primera vez para América Central. Se describe *Jaltomata darcyana*, una nueva especie de la región de la costa estacionalmente seca del Pacífico de Costa Rica; tiene filamentos rectos, anteras de tamaño variable en cada flor, estilos curvados, y crece entre 0–320 m. Las dos primeras especies son protóginas: la dehiscencia de las anteras ocurre un día después la apertura de la flor. Por otro lado, *J. darcyana* no tiene una fase pistilada y es funcionalmente hermafrodita al abrirse la flor. Se reporta por primera vez el número de cromosomas de *J. darcyana*: $2n = 24$. Se incluye una clave para el género *Jaltomata* en Costa Rica.

Key words: Costa Rica, epiphyte, *Jaltomata*, Solanaceae.

This study is part of ongoing research on the systematics of *Jaltomata* Schlttdl. (Mione et al., 1993, 1994, 2000a, 2000b; Mione & Bye, 1996). The genus *Jaltomata* includes two groups: (a) an herbaceous lineage having rotate corollas and black (rarely green) fruits, distributed from Arizona, U.S.A., to Bolivia, and (b) a woody lineage having campanulate, tubular, and rotate corollas and orange to red fruits, with its center of diversity in the Andes but with one species each in the Greater Antilles and the Galápagos Islands. This study was conceived in the early 1990s when T.M. realized that the *Flora of Costa Rica* (Standley, 1937) listed only a single species of *Jaltomata*, but herbarium specimens from the country exhibited more morphological and ecological variation than is normally present in one species.

The combination of attributes that distinguish *Jaltomata* from other Solanaceae genera is: simple leaves, distinct peduncles, umbellate inflorescences, accrescent calyces that spread over the berry but never enclose it nor completely hide it in side view, filaments expanded at base, longitudinal anther dehiscence, and an ovarian nectar disk. Additional features present in (but not limited to) Costa Rica are: herbaceous habit, angular stems, a rotate corolla, microscopic glands (having unicellular stalks and multicellular heads) on the abaxial faces of the perianth, yellow anthers, clear nectar, and purple to black berries.

Prior to this study only a single species of *Jaltomata* was recognized in Costa Rica, though the genus grows from sea level to 2900 m elevation, from low-altitude seasonally dry forests to high-altitude consistently wet forests.

MATERIALS AND METHODS

Fieldwork in Costa Rica was done by T.M. in 1994, and by T.M. and L.Y. in 1995 and 2000. In the field plants were pressed, flowers were placed in 70% ethanol, leaves were desiccated for later DNA extraction, and habitat and locality data were recorded. Accessions from throughout the range of the genus have been grown in Connecticut for study since 1990.

Principal components analysis (PCA) is a widely used multivariate technique that can reveal hidden groupings (Quicke, 1993) and allows one to consider a mixture of uncorrelated and correlated variables (Goodman, 1974). The principal components are new, uncorrelated variables each of which is a linear combination of the original variables (Kleinbaum et al., 1988). PCA was performed on the correlation matrix using Minitab (1995), with each collection representing an OTU. Some collections studied in the living condition (Table 1) were not used in the PCA because of missing data. The characters used for PCA are listed in Table 2. The collections used for PCA are listed in Table 3, where means are based on 2 to 20 observations. Until now all *Jaltomata* of Costa Rica were considered a single species, *J. procumbens* (Cav.) J. L. Gentry, and so for comparison we included *J. grandiflora* (B. L. Rob. & Greenm.) D'Arcy, Mione & Davis, a morphologically distinct species from Mexico. Measurements were made with a dissecting microscope on living, pressed, and alcohol-preserved specimens.

Trichomes are not gland-tipped unless indicated as such. Finger hairs are uniseriate, unbranched, and multicellular. Branchlet hairs have multiple termini (Seithe, 1979). Gland-tipped finger hairs (on the *Jaltomata* of Costa Rica found only on the adaxial face of the corolla) have an expanded terminal cell that stains densely with neutral red. As well, the multicellular head of the stalked glands (common on the abaxial faces of the perianth) also stains densely with neutral red. Pollen grain diameter was measured after staining pollen 30 minutes in "cotton blue" stain; anthers were stored in 70% ethanol prior to staining. Floral phenology was observed in the field, and on healthy plants grown for study both outdoors and indoors under lights. Pollen grains were counted using the method of Anderson and Symon (1989). The ovule count of one locule was doubled to obtain the total ovules per ovary. Chromosomes were counted with the method of Bernardello and Anderson (1990); to obtain root tips seeds were sown on wet filter paper in a petri dish at room temperature under ambient light.

RESULTS

The first principal component accounts for 34.8% of the total variance (eigenvalue 6.27 divided by the sum of the eigenvalues, the latter the same as the number of original variables, 18). The second principal component has variance 2.84 and explains an additional 15.8% of the total variance. A plot of principal components one and two is presented as Figure 1. The third principal component has variance 2.5 and explains another 13.9% of the total variance. The first three components explain 64.5% of the variation; the first seven principal components explain 91% of the variation. The first principal component shows the highest loadings (Table 2) for characters that are among the most valuable for diagnosing species (see also key), e.g., characters: 9—filaments straight versus sigmoid, 11—the presence or absence of anther size variation within the flower, and 14—style straight versus curved. This is not surprising because the first component is the linear combination of the original variables that “best discriminates (produces the maximum distance) between individuals of a sample” (Pimentel, 1979). In a strict consensus tree (Mione, unpublished) based on DNA sequences (nuclear ribosomal DNA internal transcribed spacers 1 and 2 and the 5.8S gene), the collections of *J. repandidentata* form a monophyletic group. As well, the collections of *J. procumbens* of Costa Rica form a monophyletic group. *Jaltomata darciana*, represented only by Mione & Yacher 694, does not group with any other Costa Rican collection(s) but instead groups with an accession from Mexico, outside of both the *J. procumbens* and *J. repandidentata* clades.

TAXONOMIC TREATMENT

Jaltomata Schltld., Index Sem. (Halle) 1838: 8. 1838. TYPE: *Jaltomata edulis* Schltld.

A clear explanation of the nomenclatural history of *Jaltomata* was presented by Gentry (1973).

In Costa Rica the following three species occur:

- (1) *Jaltomata darciana* Mione, described below
- (2) *Jaltomata procumbens* (Cav.) J. L. Gentry
- (3) *Jaltomata repandidentata* (Dunal) Hunz.

Jaltomata procumbens has straight filaments (Fig. 2C), anthers of uniform size that, in Costa Rica, are usually mucronate (Fig. 3F), and straight styles. This species grows from 1000 to 2900 m elevation. Plants grow to 2 m high in the upper part of this altitudinal range (field observations and herbarium specimen labels). *Jaltomata repandidentata*, on the other hand, has sigmoid filaments (Figs. 2E, 3A), anthers varying in size within the flower (Fig. 2D), and curved styles (Fig. 2D, E). This species grows from 400 to 1200 m elevation; plants grow to 1 m high. Flowers of these two species are protogynous, with filament elongation and anther dehiscence occurring on the second day the flower is open. In contrast, the collection made on the seasonally dry Pacific Coast, on the Nicoya Peninsula (Mione & Yacher 694), is distinct and is characterized by straight filaments, anthers of unequal size (when mature but undehisced), curved styles, absence of a pistillate phase, and is here designated a new species.

Jaltomata darciana Mione, sp. nov. TYPE: Costa Rica. Nicoya Peninsula, Curú, 9°46'50"N, 84°56'05"W, 98 m, edge of pasture, 11 Jan. 2000, T. Mione & L. Yacher 694 (holotype, NY!; isotypes, CONN!, CR!, MO!). Figures 2A, B, 3C, D.

Herba, caulibus insigniter angulatis, foliis ad 30 cm longis, inflorescentiis floribus 23 ut maxime, calyce aequabiliter viridi, corolla rotata, filamenta recta, antheris non mucronulatis, stylo curvo dirigente stigma ad latus, floribus numquam non hermaphroditis.

Erect glabrous herb to 1 m (described as 1.5 m on Janzen 12125) high. Stems hollow, green to purple, strongly angulate with 4 or 5 raised longitudinal ridges (Fig. 2A), to 2.5 cm diam. at base. Leaves alternate, often geminate, the blade elliptic, somewhat coriaceous, the faces

TABLE 1. Living *Jaltonmata* collections studied.

Species	Country	Locality and elevation	Collector & #, and accession number, where applicable	Herbaria	Seen in the field	Grown for study in U.S.A.
<i>J. darcyana</i>	Costa Rica	Nicoya Peninsula, Curú, 98 m	Mione & Yacher 694 (holotype)	CONN, CR, MO, NY	x	x
<i>J. grandiflora</i>	Mexico	Michoacán, Patzcuaro area, 2073 m	Davis 1114, Mione accession 454	COLO, CONN, F, MEXU, MO		x
<i>J. procumbens</i>	Costa Rica	Copey, 1740 m	Sawyer 623, Mione accession 395	INB		x
<i>J. procumbens</i>	Costa Rica	Border of Puntarenas and Alajuela, Cordillera de Tilarán, Monteverde Cloud Forest Reserve (on the Continental Divide at "La Ventana"), 1560 m	Mione 583	INB, MO	x	x
<i>J. procumbens</i>	Costa Rica	same as 583	Mione & L. Coe 606	INB, NY	x	x
<i>J. procumbens</i>	Costa Rica	Parque Nacional Tapantí, 1420 m	Mione & Yacher 684	CONN	x	
<i>J. procumbens</i>	Costa Rica	Parque Nacional Tapantí, 1418 m	Mione & Yacher 685	CONN	x	
<i>J. procumbens</i>	Costa Rica	Parque Nacional Tapantí, 1744 m	Mione & Yacher 686	CONN	x	
<i>J. procumbens</i>	Costa Rica	Parque Nacional Tapantí, 1744 m	Mione & Yacher 687	CONN	x	
<i>J. procumbens</i>	Costa Rica	Parque Nacional Tapantí, 1763 m	Mione & Yacher 688	CONN	x	
<i>J. procumbens</i>	Costa Rica	Copey, 1740 m	Mione & Yacher 689	CONN	x	
<i>J. procumbens</i>	Costa Rica	Santa Maria, 1905 m	Mione & Yacher 690	CONN	x	
<i>J. procumbens</i>	Costa Rica	Estación Cuericí, 2600 m	Mione & Yacher 692	CONN	x	
<i>J. procumbens</i>	Costa Rica	Volcán Turrialba, 2700 m	Mione & Yacher 693	CONN	x	
<i>J. procumbens</i>	Costa Rica	Monteverde, 1500 m	Mione & Haber 697	CONN	x	
<i>J. procumbens</i>	Costa Rica	Monteverde, 1500 m	Mione & Haber 698	CONN	x	
<i>J. procumbens</i>	Costa Rica	Zarceo, 1650 m	Mione et al. 699	CONN	x	
<i>J. procumbens</i>	Costa Rica	Escazu, 1410 m	Mione & Yacher 700	CONN	x	
<i>J. procumbens</i>	Costa Rica	Río La Paz Pequeña, 1375 m	Bohs seed 95-4, Mione accession 635	CONN		x

<i>J. procumbens</i>	Costa Rica	Catarata San Luis, 1180 m	<i>Bohs seed 96-49</i> , Mione accession 636	INB	x
<i>J. procumbens</i>	Guatemala	Chiquimula, 1930 m	<i>Spooner et al. 7038</i> , Mione accession 321	AGUAT, BIGUA	x
<i>J. procumbens</i>	Mexico	Morelos, mpio. Tetela del Volcán, 2200 m	<i>Bye & Linares 10219</i> , Mione accession 456	MEXU	x
<i>J. procumbens</i>	Mexico	Mexico, rd. from Rt. 130 (134) to Valle de Bravo, 2600 m	<i>Mione 593</i>	CONN	x
<i>J. procumbens</i>	Mexico	Chiapas, Tzabalhó, 1650 m	<i>Eber s.n.</i> , Mione accession 401	CONN	x
<i>J. procumbens</i>	Mexico	Puebla, San Miguel Tenexatiloyan, 2500 m	<i>Mione 586</i>	CONN	x
<i>J. procumbens</i>	Mexico	Morelos, mpio. Tepoztlán, 1 km W of La Pera on Hwy. 95D, at rest stop, 2230 m	<i>Mione & Bye 599</i>	CONN	x
<i>J. procumbens</i>	Mexico	México, Valle de Bravo, rd. from 130 (134) to Valle de Bravo, 2500 m	<i>Mione & Basurto 596</i>	CONN	x
<i>J. repandidentata</i>	Bolivia	La Paz, Nor Yungas, 4.5 km below Yalosa then 13.7 km W on road up Río Huarinilla, 1200 m	<i>Mione et al. 565</i>	CONN, NY	x
<i>J. repandidentata</i>	Costa Rica	Puntarenas: Cordillera de Tilarán, along rd. from Carretera Interamericana to Monteverde, 700 m	<i>Mione & Yacher 605</i>	INB, NY, UT	x
<i>J. repandidentata</i>	Costa Rica	San Isidro, 580 m	<i>Mione & Yacher 691</i>	UT	x
<i>J. repandidentata</i>	Costa Rica	Santa Elena, 1180 m	<i>Mione & Haber 696</i>	UT	x
<i>J. repandidentata</i>	Mexico	Guerrero, 58 km from Atoyac de Alvarez on rd. to Puerto de Gallo, 1021 m	<i>Davis 822</i> , Mione accession 362	CONN, MO	x
<i>J. repandidentata</i>	Mexico	Veracruz, along old rd. 150 between Orizaba and Fortín; shade of coffee bushes, 1097 m	<i>Dean 266</i> , Mione accession 571	XAL	x
<i>J. repandidentata</i>	Nicaragua	Granada, Volcán Mombacho, common erect weed in coffee plantation, 450 m	<i>Mione & Coe 555</i>	CONN, HNMH, NY	x

TABLE 2.

Characters used in principal components analysis and component loadings (eigenvectors) on the first three components.

Character	PC1	PC2	PC3
1 Altitude of collection locality	-0.286	-0.290	-0.061
2 Leaf margin: ranked from entire [0] to highly toothed [1]	0.122	-0.017	-0.107
3 Leaf vestiture of adaxial face: ranked from glabrous [0] to densely pubescent [1]	-0.169	-0.179	-0.402
4 Mean peduncle length maximum	-0.039	0.247	0.018
5 Flower: not protogynous [0], protogynous [1]	-0.110	-0.220	-0.115
6 Mean calyx diameter during anthesis	0.208	-0.222	0.350
7 Sepals reflexed during hermaphroditic phase: no [0], somewhat [1], strongly [2]	-0.024	-0.414	0.238
8 Number of corolla lobes: 5 lobes and no lobules [0], both 5 lobes and 5 lobules [1]	-0.096	-0.001	-0.521
9 Filaments: straight [0], sigmoid [1]	0.345	0.024	-0.064
10 Mean filament (including expanded base) length when fully elongated	0.288	-0.209	-0.208
11 Anther size variation within flower: absent [0], present [1]	0.368	0.141	0.006
12 Mean anther length (undehisced, living and/or preserved in 70% ethanol)	0.264	-0.356	-0.041
13 Anthers: lacking mucro [0], mucronate or mucronulate [1]	-0.217	0.278	0.256
14 Style: straight [0], curved [1]	0.368	0.141	0.006
15 Stigma: no groove [0], shallow groove [1], bilobed [2]	0.275	0.140	0.110
16 Mean style length (living and/or preserved in 70% ethanol)	0.274	-0.309	-0.215
17 Mean stigma diameter	-0.087	-0.373	0.430
18 Mean % of the filament (incl. expanded base) that bears hairs, proximal to distal	-0.246	-0.109	-0.034

TABLE 3.

Data used in principal components analysis: collection numbers are as in Table 1 and characters are numbered as in Table 2; *dar*, *Jaltomata darciana*; *gran*, *J. grandiflora*; *proc*, *J. procumbens*; *repa*, *J. repandidentata*.

TABLE 3.

Data used in principal components analysis: collection numbers are as in Table 1 and characters are numbered as in Table 2; darc, *Jaltomata darciana*; gran, *J. grandiflora*; proc, *J. procumbens*; repa, *J. repandidentata*.

Species	Character Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
darc	694	98	0	0	27	0	12.5	0	0	0	4.4	1	1.9	0	1	1	4.2	0.5	12
gran	454	2073	1	1	15	1	17.0	1	0	0	4.4	0	3.0	0	0	0	5.2	1.1	50
proc	321	1930	1	1	52	1	8.3	0	1	0	6.2	0	1.9	0	0	0	5.4	0.3	55
proc	401	1650	1	1	62	1	11.5	0	0	0	5.1	0	2.8	0	0	0	5.0	0.5	15
proc	456	2200	0	1	29	1	7.0	0	1	0	4.9	0	1.9	0	0	0	4.0	0.5	30
proc	583	1560	0.2	0	70	1	12.3	0	0	0	4.1	0	1.6	1	0	1	3.1	0.6	29.8
proc	586	2500	0	0.1	27	1	11.1	0	0	0	6.1	0	2.4	0	0	0	4.9	0.8	15
proc	593	2600	0	1	30	1	8.1	0	1	0	4.6	0	2.0	0	0	1	3.8	0.4	37
proc	596	2500	0	0	34	1	10.6	1	0	0	5.1	0	2.0	0	0	1	4.1	1.0	24
proc	599	2230	0	0	43	1	17.0	0	0	0	6.5	0	2.8	0	0	1	4.9	0.6	15
proc	635	1375	0.6	0	75	1	12.0	0	0	0	3.4	0	1.8	1	0	1	3.0	0.7	27.3
proc	636	1180	1	1	25	1	10.9	0	0	0	4.2	0	1.6	0	0	0	3.5	0.7	60
proc	689	1740	1	1	50	1	9.1	0	0	0	3.3	0	1.7	1	0	0	3.6	0.6	42.5
proc	692	2600	0	1	31	1	10.3	0	0	0	5.7	0	1.8	1	0	0	4.9	0.7	47
proc	693	2700	0	0.2	35	1	14.5	0	0	0	4.4	0	1.5	1	0	0	3.5	0.7	88
proc	699	1650	0.7	0.2	28	1	10.3	0	0	0	3.6	0	1.7	1	0	0	2.9	0.6	30
proc	700	1410	0.7	0.3	27	1	8.6	0	0	0	3.3	0	1.7	1	0	0	2.8	0.6	20
repa	555	450	1	0.1	35	1	13.1	0	0	1	6.9	1	2.6	0	1	2	5.4	0.5	15
repa	605	700	1	0	33	1	14.6	0	0	1	6.8	1	2.7	0	1	1	6.1	0.5	15
repa	691	580	1	0.3	37	1	14.5	0	0	1	7.2	1	2.6	0	1	1	5.2	0.6	10

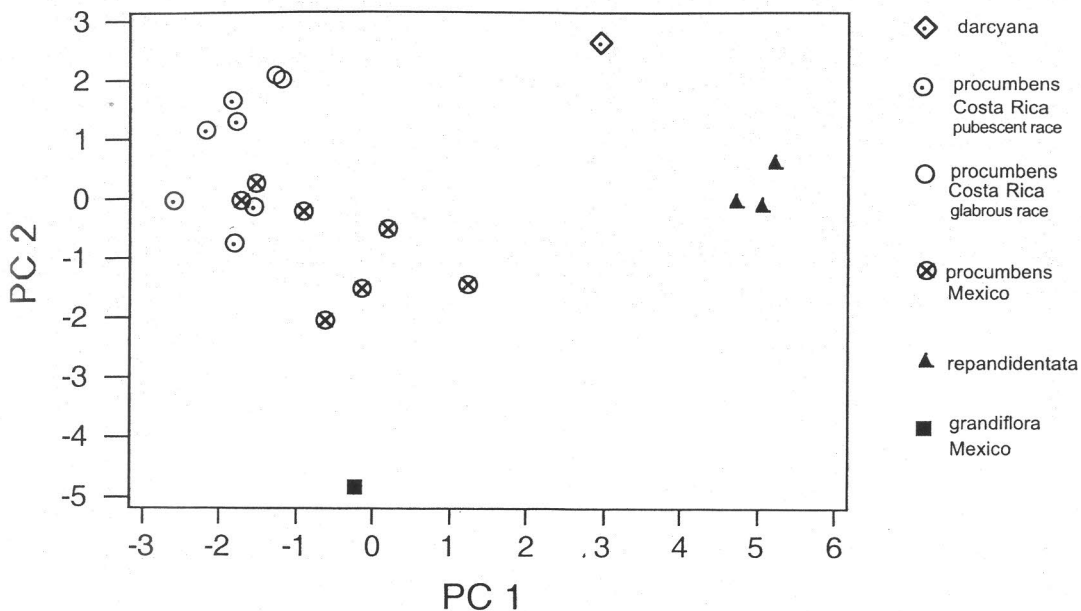


Figure 1. Plot of principal components one and two using 18 morphological characteristics. Each plotted point represents a collection listed in Table 3.

glabrous and lustrous, to 30 cm long, the length to width ratio 1.5–1.8, the proximal 13%–16% of the blade cuneate, the tip usually acuminate (Fig. 2A), the margin entire or nearly so and on smaller, younger leaves sparsely ciliolate with finger hairs to 0.1 mm long; petiole to 2.5 cm long. Inflorescence axillary or arising from a stem dichotomy, umbellate, to 23-flowered. Peduncle to 2.1 cm long and pedicel to 2.3 cm long; both green, glabrous, and with raised longitudinal ridges. Calyx during anthesis: green, 5.2–7.4 mm from pedicel to tip of lobe, 12–14 mm diam., the midrib raised, ciliolate near apex with 1- to 3-celled finger hairs 38–138 μ m long, the hairs usually simple but occasionally with more than one terminus, abaxially with abundant stalked glands 60–75 μ m long. Calyx at fruit maturity: to 26 mm diam., stellate, green, rotate to slightly reflexed, not hiding fruit in side view. Corolla (Fig. 2B) rotate, light green with dark-green maculae collectively stellate in outline, 5-lobed, 17–20 mm (–25 mm, cultivated) diam., the margin ciliolate with branchlet hairs to 190 μ m long, adaxially densely pilosulose with erect, gland-tipped (droplet-tipped on fresh flowers) finger hairs, (4)5- to 6-celled and

210–290 μ m long, abaxially with abundant stalked glands 70–80 μ m long. Stamens (Fig. 3C) 4.5–5 mm long; filaments straight or nearly so, nearly glabrous with unpigmented finger hairs to 0.3 mm long only on expanded base; anthers (Fig. 3D) 1.4–1.9 \times 1.0–1.8 mm, yellow. Pollen 25–27.5 μ m diam. ($n = 59$ grains); 74,000–149,000 grains per androecium ($n = 2$ androecia). Stigma green, capitate, with a shallow medial groove (when living), 0.33–0.51 mm wide (when pressed), the papillae to 28 μ m long (living); style 4.2–5.1 mm long, curving and so orienting the stigma to the side (Fig. 2B); ovary dark green with an off-white to light orange disk girdling the base, glabrous; 158–168 ovules per ovary ($n = 2$ ovaries). Mature berries dark black-blue, subspherical, to 14 mm diam. (similar to Fig. 2F). Seeds subovate, alveolate, 1.8–1.98 \times 1.41–1.62 \times 0.45–0.54 mm thick, to 146 per fruit. Chromosome number $2n = 24$.

Paratypes. COSTA RICA. **Guanacaste**: Santa Rosa National Park, ca. 10°50'N, 85°37'W, 0–320 m, 16 July 1981, *Janzen 12113* (MO); 10°50'N, 85°35'W, 8 Nov. 1981, *Janzen 12125* (F); Nicoya Peninsula, Cantón Nandayure, Pilas de Bejuco, Quebrada Seca, 9°52'01"N, 85°20'45"W, 40 m, 15 Oct. 1994,

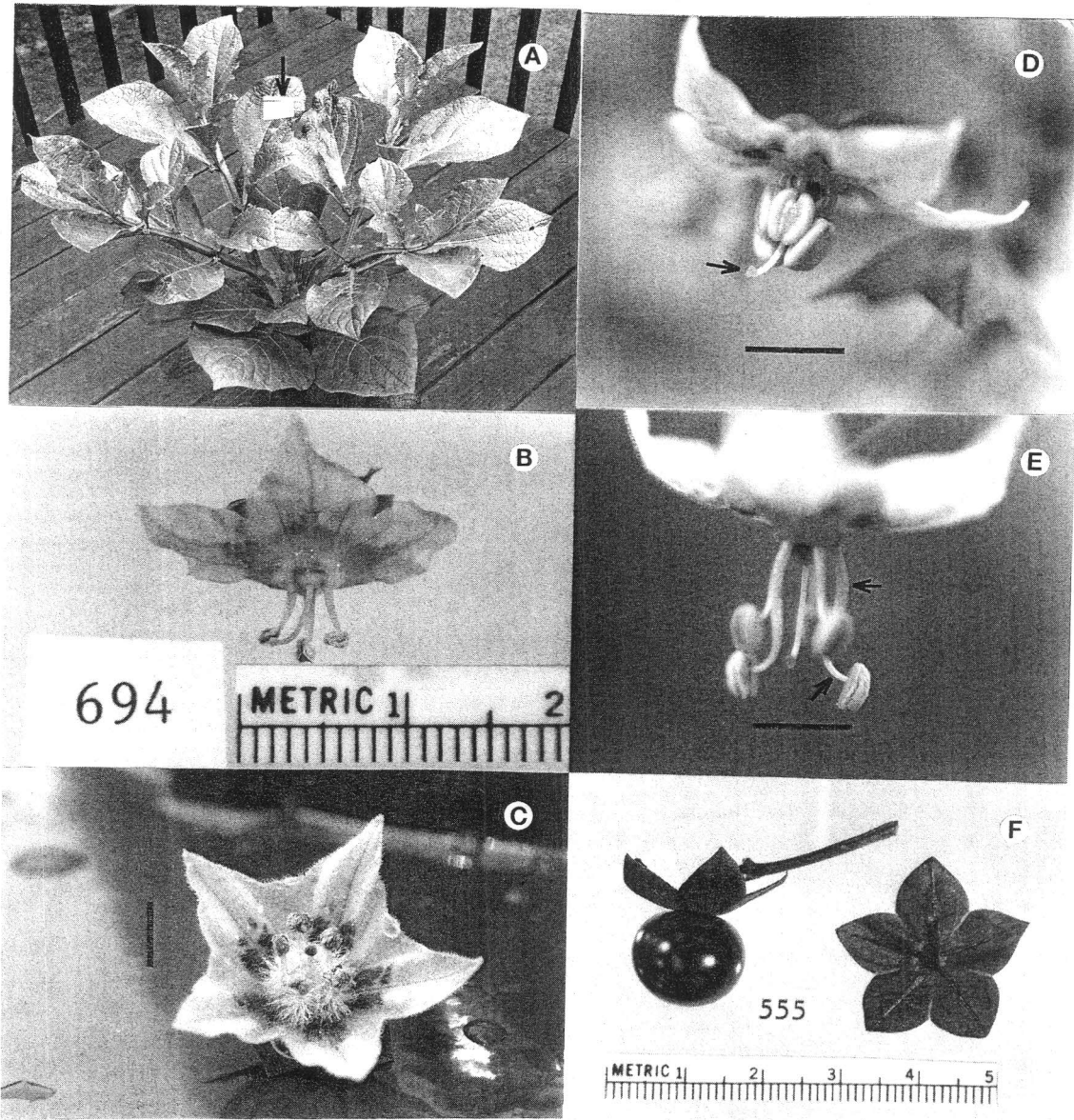


Figure 2. *Jaltomata* of Costa Rica. A, B. *J. darcyana*, Mione & Yacher 694. —A. Note erect habit, nearly entire leaves, and strongly angled stems. White scale bar (at arrow) = 6 cm. —B. Flower with two stamens removed to show curved style; note nectar where androecium meets corolla. —C. Flower of *J. procumbens*, Bohs' seed 96-49. Note the straight style and straight filaments; anthers have dehisced; stigma at center; bar = 5 mm. D, E, F. *J. repandidentata*. —D. Mione & Yacher 605. Flower in pistillate phase: the first day the flower is open filaments remain short and anthers undehisced; note anther size variation, variation in length of stamens, curved style orienting bilobed stigma (at arrow) to side; bar = 5 mm. —E. Mione & Yacher 605. Hermaphroditic phase, filaments have elongated and those of the longer stamens are sigmoid; two arrows point to one filament; the anthers of the longest stamens have dehisced; style curving stigma toward viewer; bar = 5 mm. —F. Mione & Coe 555. Black-purple berry with calyx (left), and calyx with abaxial face and pedicel showing (right).

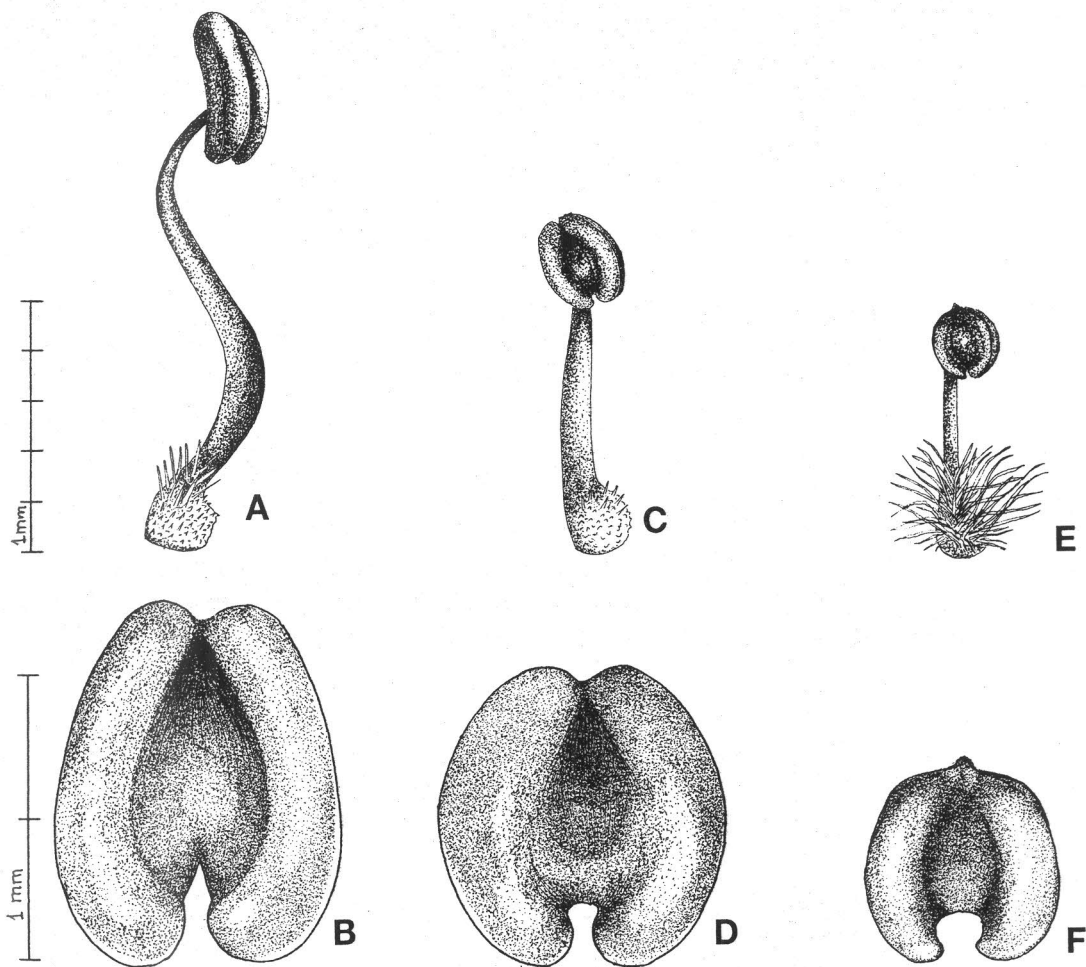


Figure 3. Stamens (tangential view) and anthers (dorsal face). A, B. *Jaltomata repandidentata*, Mione & Yacher 605. — A. Sigmoid filament with anther. —B. Anther. C, D. *J. darciana*, Mione & Yacher 694. —C. Nearly straight filament with anther. —D. Anther. E, F. *J. procumbens*, Mione et al. 699. —E. Straight filament with mucronate anther. —F. Mucronate anther. Illustration by Luis Serazo.

Estrada & Rodríguez 242 (CR, INB). **Puntarenas:** Reserva Biológica Carara Estación Quebrada Bonita, 9°46'N, 84°36'W, 30 m, 26 June 1990, *Bello & Rojas 2295* (CR, F, INB); Nicoya Peninsula, Curú, pastures S of entrance road, mouth of Marianas Canyon, 50 m, 13 Sep. 1995, *Sanders & Baker 17892* (F, NY).

REPRODUCTIVE BIOLOGY OF *JALTOMATA DARCYANA*

This species is self-compatible and autogamous, based on abundant fruit production by spatially isolated plants grown for study in 2000, 2001, and 2002. Translucent nectar droplets were observed where the corolla and androecium meet (Fig. 2B). This nectar is very likely produced by the ovarian disk and then, taking the path of least resistance, seeps through the bases of the stamens on to the corolla. Flowers of this species last only a single day during which they are functionally perfect.

Jaltomata procumbens (Cav.) J. L. Gentry, *Phytologia* 27: 287. 1973. *Atropa procumbens* Cav., *Icon. Pl.* 1: 53, t. 72. 1791. *Saracha procumbens* (Cav.) Ruiz & Pav., *Fl. Peruv. Prodr.* 2: 43. 1794. TYPE: Cavanilles, *Icon. Pl.* 1: 53, t. 72. 1791 (lectotype, designated here).

Jaltomata edulis Schldl., *Hortus Halensis* 8. 1838. TYPE: "Prope los baños del grande indefessus C. Ehrenberguis fructiferam Octoberi mense carpsit," *Ehrenberg, s.n.* (not seen).

In Costa Rica *Jaltomata procumbens* (Figs. 2C, 3E, F) is common at higher elevations along the edges of trails and roads. This species is somewhat scattered in Figure 1 because of the morphological variation present among the collections utilized from a large geographic area (Mexico, Guatemala, and Costa Rica). In Mexico it is a common weed in agricultural fields where it is deliberately not weeded out so that fruits can be gathered for consumption (Davis & Bye, 1982) and sometimes sold in markets (R. Bye, pers. comm.).

Two races of *Jaltomata procumbens* grow sympatrically, and were found only 4 m apart in Parque Nacional Tapantí (hereafter, Tapantí).

One race is glabrous and has longer peduncles (to 6 cm) and nearly entire leaves. This race is common along the edge of the gravel road in Tapantí (*Mione & Yacher 687*) and was found on the Continental Divide at Monteverde (*Mione 583, 606*), observed along trails in the Santa Elena reserve (not collected), and was collected at Río La Paz Pequeña (*Bohs 95-4*). The other race, in contrast, is pubescent and has shorter peduncles and toothed leaves. This race was collected at Tapantí (*Mione & Yacher 686, 688*), and in the Monteverde area: (1) at Catarata San Luis (*Bohs 96-49*), (2) as an epiphyte in the primary forest (*Mione & Haber 697*), and (3) outside the main reserve on a road bank (*Mione & Haber 698*). The two collections of the glabrous race used in the PCA group together (Fig. 1). The epiphytic *J. procumbens* collected (pubescent race) was a light gap colonist in a primary Tropical Lower Montane Wet Forest at Monteverde (W. Haber, pers. comm.; see Holdridge et al., 1971). It is clear that the races have overlapping niches, and further study will be necessary to determine the taxonomic level, if any, at which these races should be recognized.

Uses. During fieldwork for this study, only at a population near the summit of Volcán Turrialba were we informed by a resident that fruits are eaten. The label of one other specimen (*Holway 283*) of this species indicates that the fruits are used in Costa Rica, and gives the local name "yerba mora."

Selected specimens examined. COSTA RICA. **Puntarenas:** Monteverde, upper community, lower montane wet forest, epiphyte herb on tree trunk, 27 Sep. 1985, *Haber 2804* (MO). **Border of Puntarenas and Alajuela:** Cordillera de Tilarán, on & near Continental Divide, ca. 2–5 km E & SE of Monteverde, along trail below windswept elfin forest, 17 Mar. 1973, *Gentry & Burger 2737* (MO). **Alajuela:** Monteverde Reserve, Atlantic Slope, Río Peñas Blancas valley, ridge trail above Quebrada Leona, forest edge, 17 Jan. 1985, *Haber 1317* (MO); Alajuela, region of Zarcero, 29 Sep. 1937, *Smith A457* (F). **Heredia:** Vara Blanca de Sarapiquí, N slope of Central Cordillera, July–Sep. 1937, *Skutch 3/88* (GH, NY, US). **San José:** along Interamerican hwy. betw. Villa Mills and San Isidro de El General, km 111, *Grayum et al. 3428* (MO); Las Nubes, 20–22 Mar. 1924, *Standley 38651* (US); Cordillera de Talamanca, reserva Privada Cerros de Escazú, Finca El Cedral, 8 Aug. 1996, *Cascante 1107* (CR, F). **Cartago:** El Muñeco, Río Navarro, 6–7 Mar. 1926, *Standley & Torres R. 1158* (US); Parque Nacional

Tapantí, along road 1.2 km after entrance, 11 Dec. 1996, *Spooner et al.* 7126 (INB not seen, WIS not seen, herbarium of T.M.); ca. 10 km S of Tapantí above Río Grande de Orosi, 10–24 June 1968, *Burger & Stolze* 5725 (F, NY); Cordillera de Talamanca, along road from bridge over Río Grande de Orosi (near jct. with Río Villegas) to Río Humo, 11 Aug. 1984, *Grayum et al.* 3743 (MO); SW slope of Volcán Irazu, W of Sabanilla, 7 Mar. 1987, *Burger et al.* 12079 (F, MO, NY); Volcán Irazu, 23 Dec. 1915, *Holway* 283 (US); Volcán Turrialba, 13 Dec. 1996, *Spooner et al.* 7132 (INB not seen, herbarium of T.M.).

Jaltomata repandidentata (Dunal) Hunz., Kurtziana 10: 8. 1977. *Saracha procumbens* var. *repando-dentata* Dunal, Prodr. 13(1): 431. 1852. *Saracha repandidentata* (Dunal) Bitter, Repert. Spec. Nov. Regni Veg. 19: 269. 1924. TYPE: Peru. *Poeppig* 1419 (holotype, F!; isotypes, G!, photo of destroyed B specimen, F neg. 2555, GH!, WIS!, W, photo of W specimen, F neg. 33015, GH!, WIS!).

This species has not been previously reported from Central America, yet it is clearly morphologically distinct (Figs. 1, 2D–F, 3A, B). Growing from Mexico to Bolivia, it is a common weed in coffee plantations, based on: (1) fieldwork by T.M. with associates in Nicaragua and Bolivia, (2) plants grown from seeds collected in the shade of coffee in Mexico (Table 1), and (3) study of herbarium specimens. In Costa Rica we collected this species in coffee plantations, and along the roadside on the Pacific slope on the way up to Monteverde.

With living material or flowers preserved in alcohol *Jaltomata repandidentata* is easily distinguished from other species of the genus. Throughout its range *J. repandidentata* is characterized by: (1) size variation among anthers of a flower, most evident during the first day the flower is open when anthers remain undehisced (Fig. 2D), (2) stamen length variation within each flower during both the initial pistillate phase when filaments are short (Fig. 2D) and the perfect phase after filaments fully elongate (Fig. 2E), (3) longer stamens finally sigmoid (Fig. 2E, 3A), (4) curved style orienting the stigma to the side (Fig. 2D, E), (5) stigma shallowly grooved to bilobed (Fig. 2D), (6) larger anthers dehisce earlier than smaller anthers of the same flower (Fig. 2E), and (7) fruit fully exposed (the

calyx does not hide it) in a view perpendicular to the pedicel at the height of the fruit (Fig. 2F). All of these features were seen on the collections of *J. repandidentata* listed in Table 1, all studied in the living condition. Unfortunately, these characters are often obscured on pressed specimens. For example, anther size variation is much less evident after anthers dehisce. Filaments usually appear curved on pressed specimens, but the straight filaments of other species may become curved during pressing. Similarly, the straight style of *J. procumbens* may become curved during pressing. Unfortunately, if a stigma is flattened during pressing it will not appear bilobed, even though grooved to bilobed stigmas are characteristic of *J. repandidentata*.

Uses. In Costa Rica the label of one specimen reads "Fruto comestible" and gives the local name "yerba de mora" (*Brenes* 12). In Guatemala plants of this species were "used as a pot herb by Indians" (*Muenschler* 12458, BH, and 12479, BH F). In Peru the fruits were described as edible (*Cowgill* 1079, BH GH).

Selected specimens examined. COSTA RICA. **Alajuela:** N of San Ramon on NE slopes at bridge over Río Barranca, in coffee plantation, 17 June 1976, *Davis* 616 (MO); Tacares, Río Prendas bridge on rt. 1 to Alajuela under coffee just before river, 18 June 1976, *Davis* 623 (MO). **Heredia:** betw. Santo Domingo and Río Virilla, 6 Jan. 1974, *Lent* 3756 (F). **San José:** Jardinería en San José, *Brenes* 12 (F); vicinity of El General, June 1936, *Skutch* 2649 (GH, K, NY, US); vicinity of El General, June 1939, *Skutch* 4373 (F, GH, K, NY, US). **Cartago:** S of San Isidro de General on Rt. 2 at Río Jilguero in coffee and banana plantations, 14 June 1976, *Davis* 613 (MO); San Isidro de General, 24 July 1940, *Chrysler* 5293 (F).

DISCUSSION

The *Flora of Costa Rica* (Standley, 1937) lists a single species of the genus *Jaltomata*, *J. procumbens*, as did Janzen and Liesner (1980) and Pittier (1908). In contrast, the results of this study support the recognition of three species of this genus in Costa Rica.

This study brings the number of recognized *Jaltomata* species of the United States (Arizona), Mexico, and Central America to six: *J.*

chiuahuensis (Bitter) Mione & Bye (northern Mexico); *J. confinis* (Morton) J. L. Gentry (Guatemala); *J. grandiflora* (Michoacán, Mexico); and the species discussed here.

Based on the results of this study a new species of the seasonally dry Pacific Coast, *Jaltomata darcyana*, is described. This species is morphologically distinct (Fig. 1), grows at lower elevations than the other species, and its DNA places it outside the clades that include *J. procumbens* and *J. repandidentata*. The flowers of all other *Jaltomata* of Mexico and Mesoamerica studied to date, some 50 collections, last at least two days and are always pistillate for a day prior to filament elongation and anther dehiscence. In contrast, *J. darcyana* has lost this initial period during which the flower cannot self-pollinate.

KEY TO THE JALATOMATA OF COSTA RICA

- 1a. Style straight; in Costa Rica calyx at flowering green with purple lobe tips and/or purple main veins; anthers of uniform size, mucronate in Costa Rica (Fig. 3E, F); mature fruit partially hidden by calyx on some collections; 1000–2900 m...*J. procumbens* (Cav.) J. L. Gentry
- 1b. Style curved (Fig. 2B, D); calyx at flowering uniformly green; anthers neither mucronate nor mucronulate, those of a flower vary in size (most evident during the first day the flower is open when anthers remain undehisced); fruit fully exposed (the calyx does not hide it) in a view perpendicular to the pedicel at the height of the fruit, as shown for *J. repandidentata* in Figure 2F.
- 2a. Leaves membranous, to 20 cm long; filaments curved to sigmoid (Fig. 2E); stigma shallowly grooved to bilobed (Fig. 2D); flowers pistillate for a day and then functionally perfect; 400–1200 m...*J. repandidentata* (Dunal) Hunz.
- 2b. Leaves somewhat coriaceous, to 30 cm long; filaments straight or nearly so (Fig. 2B); stigma with a very shallow medial groove; flowers functionally perfect when they open; 0–320 m...*J. darcyana* Mione

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The specific epithet "*darcyana*" was chosen to honor William D'Arcy. Bill generously and patiently shared his expertise and treated me like a valued colleague even when I was a novice researcher. Bill will always be remembered and always be missed. T.M.

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