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Jaltomata tlaxcala, a new species of the genus *Jaltomata* (Solanaceae, Solanoideae, Solaneae)

IGNACIO DARÍO FLORES-SÁNCHEZ[1,4], MANUEL SANDOVAL-VILLA[1,5], EBANDRO USCANGA-MORTERA[2,6] & HILDA VICTORIA SILVA-ROJAS[3,7]*

[1]*Postgraduate in Edaphology, Colegio de Postgraduados, Mexico-Texcoco Highway, km 36.5, Montecillo, Texcoco 56264, Mexico*
[2]*Postgraduate in Botany, Colegio de Postgraduados, Mexico-Texcoco Highway, km 36.5, Montecillo, Texcoco 56264, Mexico*
[3]*Postgraduate in Seeds Production, Colegio de Postgraduados, Mexico-Texcoco Highway, km 36.5, Montecillo, Texcoco 56264, Mexico*
[4] *flores.ignacio@colpos.mx; https://orcid.org/0000-0003-3425-7480*
[5] *smanuel@colpos.mx; https://orcid.org/0000-0002-0228-0734*
[6] *uscanga@colpos.mx; https://orcid.org/0000-0002-8951-8724*
[7] *hsilva@colpos.mx; https://orcid.org/0000-0002-9567-0861*
**Author for correspondence*

Abstract

The taxonomic status of a specimen of the genus *Jaltomata* recovered from the Central Highland Valley of Mexico was realized. Phylogenetic analysis was performed via Bayesian inference and maximum likelihood methods complemented with Genealogical Concordance Phylogenetic Species Recognition (GCPSR) using the PHI test. The results indicated that the specimen in study belongs to the genus *Jaltomata sp. nov*. supported by PHI test (φ=1.0) showing no evidence of recombination. Characteristics of corolla, pedicel and calyx, stigma, anthers, fruit, and seeds, differentiated this species. Based on the results, the name *Jaltomata tlaxcala* is proposed for this new species.

Key words: Decumbent, DNA sequencing, green fruit, phylogenetic tree

Introduction

Taxonomic characterisation of plant species diversity remains a major and substantial challenge with an estimated 70,000 species of flowering plants awaiting discovery, and there is a need to update taxonomic records and to assign unidentified specimens to known species, which is relevant when optimal material is not available or when available levels of taxonomic expertise are low (Hollingsworth *et al*. 2016).

In Mexico, there are about 23,000 native species of vascular plants, of which the knowledge of their geographical distribution is still deficient, and in some regions of the country, the number of species is underestimated, therefore, filling gaps in the information can improve the floristic knowledge, especially in materials that have been collected and entered into herbaria but have not been curated at the species level (Murguía-Romero *et al*. 2021), or that have not been clearly assigned, as in the case of specimens of the subgenus *Leptostemonum*, of the genus *Solanum*, whose infrageneric classification is complicated, despite research based on phylogenetic and morphological studies (Cuevas-Guzmán & Núñez-López 2015).

In the genus *Jaltomata* Schltdl. in Leiva *et al*. (2017: 121), belonging to the family Solanaceae (Mione *et al*. 2015a), a similar situation is reported, as it is difficult to distinguish morphologically between species belonging to the genus (Mione & Bye 1996; Mione *et al*. 1994). For example, in Mesoamerican species, in the case of living specimens of the two identified forms of *Jaltomata chihuahuensis* (Bitter) Mione & Bye (1996: 78), in the absence of mature fruits they appear to be morphologically indistinguishable (Mione & Bye 1996); on the other hand, with dried specimens, *Jaltomata grandiflora* (Robinson & Greenman) D´Arcy, Mione & Davisin D´Arcy *et al.* (1992: 190) is the only easily distinguishable species (Mione *et al*. 1994), being differentiated by its large pentagonal spotted flowers, stems and smooth, velvety leaves (D'Arcy *et al*. 1992).

Two diversity centres of the genus *Jaltomata* are recognized, South America and Mexico, with around 63 and 7 species, respectively (Mione *et al*. 2015a). It is distributed from the southwestern United States, Mexico, Central and

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South America. Later, it was spread to Haiti, Cuba, Jamaica, Dominican Republic, Puerto Rico, and the Galapagos Islands; it grows at altitudes near sea level to above 4,100 m (Davis & Bye 1981; Mione *et al.* 2007). Species are herbaceous and shrubby, with edible fruits (Mione *et al*. 2015a); South American species are distinguished from those of Central America and Mexico by their growth habit and fruit colour. The former, almost all woody, produce primarily red and orange fruit (Mione *et al*. 1994), while the latter are herbaceous and mainly bear purple or black fruits (Mione *et al*. 2015b).

For Mexico, seven species of *Jaltomata* are reported: *Jaltomata bohsiana* Mione & D.M. Spooner in Mione & Spooner (2010: 186); *J. chihuahuensis* (Bitter) Mione & Bye; *J. grandiflora* (Robinson & Greenman) D´Arcy, Mione & Davis; *Jaltomata repandidentata* (Dunal) Hunz. in Powell (2007: 14); *Jaltomata procumbens* (Cav.) J.L. Gentry in Davis & Bye (1981: 225); *Jaltomata oaxaca* and *Jaltomata chiapensis* (Unpublished data, Mione, pers. comm. 2019).

In addition, specimens restricted to specific regions are found in the country, such as *J. grandiflora*, which is considered rare as only three collections have been recorded from Patzcuaro, Michoacan, Mexico (D'Arcy *et al*. 1992). Also, in Tlaxcala, Mexico, a population is found that is distinguished by its decumbent growth habit and green fruit at maturity, tentatively assigned to *J. procumbens* (Mione *et al.* 1994). However, based on characteristics such as growth habit, flower and fruit, and the number of seeds, it could be recognized as a distinct species, such as *J. tlaxcala* (Coe 1997; Mione 1992); or considered a variety of *J. procumbens* (Mione, pers. comm. 2019).

However, the number of *Jaltomata* species reported for Mexico with detailed descriptions and herbarium material considers between one and three taxa: in Flora of the Bajio and Adjacent Regions (Martínez *et al.* 2020) only three species are found: *J. grandiflora*, *J. procumbens*, and *Jaltomata* sp.; in Flora of Veracruz (Nee 1986) and Phanerogamic Flora of the Valley of Mexico (Rzedowski & Rzedowski 2010) only the taxon *J. procumbens* is registered (Mione & Spooner 2010). Furthermore, in the "CHAPA" Herbarium of the Colegio de Postgraduados, Mexico, only *J. procumbens* has been recorded, even though it has specimens that report differences in flower and fruit colour. This situation leads an underestimation of the number of *Jaltomata* species presented in the country, which could not be determined by the difficulty of morphologically distinguishing the different species.

In this situation, molecular techniques can help to solve this problem. They have been used in the systematics of families such as Solanaceae, including restriction site mapping and DNA sequencing (Bohs & Olmstead 1999). These techniques, used in molecular systematics, are based on the alignment of similar DNA sequences and the subsequent generation of inferred phylogenetic trees (Dodsworth *et al*. 2016). A technique that has been used to carry out phylogenetic relationships within and between genera (Spooner *et al*. 1993), such as that reported in *Jaltomata* (Mione *et al.* 1994). However, only some studies still consider molecular techniques to contribute to filling the gaps in this genus.

Therefore, the present research was aimed at applying DNA sequencing and generating phylogenetic trees to define the taxonomic status of the *Jaltomata* specimen with a decumbent growth habit and green fruit at maturity.

Materials and methods

Collection of vegetal material

The work was carried out in April 2020. The genetic material of the *Jaltomata* specimen, object of study in this work, and named as *J. procumbens* decumbent (Jpd), collected in the state of Tlaxcala, Mexico, was used. The specimen voucher (number 155,095) was deposited in the "Herbario-Hortorio CHAPA" of the Colegio de Postgraduados, Campus Montecillo, Texcoco, State of Mexico.

The plant tissue was obtained from plants maintained in greenhouses and used in experimental work to evaluate the agronomic characters of the specimen (Flores-Sánchez *et al.* 2021).

DNA extraction

The DNA extraction was performed using 0.5 g of *Jaltomata* young leaves and grounded in liquid nitrogen to a fine powder. The fine powder was transferred to a 2 mL Eppendorf tube with 1.2 mL of 2% cetyltrimethylammonium bromide (CTAB) (Doyle & Doyle 1990) and the sample was homogenised. Tubes were incubated in a water bath at 96 °C for 90 min, mixed at 30 min intervals, and allowed to cool at the end. Later, 500 µL of chloroform-isoamyl alcohol

(24:1) was added and mixed by inversion at room temperature for 10 min, after that, centrifuged at 11,150 × g for 10 min. The aqueous phase was transferred to fresh 2 mL tubes, 700 µL of chloroform-isoamyl alcohol (24:1) was added and mixed by inversion at room temperature for 10 min. Centrifuged again at 11,150 × g for 10 min, the aqueous phase was transferred to new 1.5 mL Eppendorf tubes, and 950 µL of cold 100% ethanol was added. It was mixed ten times, gently by inversion and incubated at -20 °C for 2 h. Centrifuged at 11,150 × g for 10 min and decanted, avoiding loss of pellet. The pellet was resuspended in 400 µL of HPLC water and incubated at 65 °C for 15 min. Then, 34 µL of 3 M sodium acetate and 1 mL of 95% ethanol were added and maintained at -20 °C for 1 h. Subsequently, the tubes were centrifuged at 11,150 × g for 10 min, and the supernatant was decanted. Later, 600 µL of 70% isopropanol was added to each tube and centrifuged at 11,150 × g for 10 min, washed twice, the supernatant was removed, and the tubes were allowed to dry for 30 min. Finally, the pellet was resuspended with 100 µL of HPLC water and spun. DNA was quantified spectrophotometrically on a Nanodrop 2000 (Thermo Scientific, USA). Good quality for PCR analysis was considered when the A260 / 280 and A260 / 230 ratios were between 1.8—2.2.

Primer design

The primer design, for the amplification of the region encompassing exons 3 through 7 of the granule-bound starch synthase (GBSSI) gene and partial cds, was performed based on the sequence downloaded from the National Centre for Biotechnology Information (NCBI): GU256339 *Jaltomata procumbens* granule-bound starch synthase (GBSSI) gene, exons 2 through 13 and partial cds. Primer3Plus software (Untergasser *et al*. 2012) was used to design the Primer3Plus package for the specimen under study (Table 1).

TABLE 1. Design primers for PCR and sequencing to identify of *Jaltomata* sp. through phylogenetic reconstruction.

Primer	Start	Length	Sequence
1 forward	3	20 bp	GTTGCGGTTGAGGTACTCCT
1 reverse	867		GGCCTTGGTAGGCAATGTTA

PCR and sequencing

The DNA was sent to Psomagen, Humanizing Genomics for amplification and sequencing (https://dna.macrogen.com/#).

Phylogenetic analysis

The sequence of the Jpd specimen was cut and assembled with Bioedit 7.2.5 (Hall 2013) and the consensus sequence was generated. This was used to obtain the sequence of maximum identity from NCBI using BLAST (Table 2). The sequences were then aligned using MAFFT v7.475 (2020, https://mafft.cbrc.jp/alignment/software/). No concatenation was performed, as no other genes were available for all the *Jaltomata* species included in this study in the NCBI database.

Phylogenetic analysis was achieved out using maximum likelihood (ML) and Bayesian inference (BI) methods. The analysis was complemented with the species *Physalis alkekengi* L. in Weese & Bohs (2007: 463), *Lycianthes asarifolia* (Kunth & Bouché) Bitter in Montani & Scarpa (2016: 28), *Solanum tuberosum* L. in Sahair *et al*. (2018: 116), and *Nicotiana tabacum* L. in Leal *et al*. (2023: 1), the latter being used as outgroup. For BI, the nucleotide substitution model was determined with jModelTest 2 (Darriba *et al.* 2012). The file for phylogenetic analysis was generated with Mesquite (Madison & Madison 2019).

BI analysis was performed with MrBayes software version 3.2 (Ronquist *et al.* 2012), with 2 numbers of substitution schemes, gamma and invariant substitution rates, and a Dirichlet distribution (1, 1, 1, 1, 1); 10,000,000 generations were performed, four Markov chains were used, sampling was achieved every 1,000 generations and the analysis was stopped when the standard deviation was less than 0.01, from which 25% of the generated trees were discarded. ML analysis was performed with the raxmlGUI-2.0.1 program (Silvestro & Michalak 2012), with the ML+rapid bootstrap method and 1,000 replicates, branch length and base frequency calculation, and the HKY + Γ+ I substitution model. The generated phylogenetic tree was visualised with FigTree v1.4.4 (https://tree.bio.ed.ac.uk/software/figtree/).

TABLE 2. GenBank accession numbers of *Jaltomata* sp. granule-bound starch synthase sequences used in this study.

Tribu	Genus	Species	Origen	Accession
Solaneae	*Jaltomata*	*J. andersonii* Mione	Peru	GU256308
		J. antillana (Krug & Urban) D´Arcy	Dominican Republic	GU256357
		J. aspera (Ruiz & Pavón) Mione	Peru	GU256332
		J. auriculata (Miers) Mione	Ecuador	GU256358
		J. bernardelloana S. Leiva & Mione	Peru	GU256330
		J. bicolor (Ruiz & Pavón) Mione	Peru	GU256289
		J. biflora (Ruiz & Pavón) Benítez	Peru	GU256302
		J. bohsiana Mione & D.M. Spooner	Mexico	GU256349
		J. cajacayensis S. Leiva & Mione	Peru	GU256298
		J. cajamarca Mione	Peru	GU256300
		J. chihuahuensis (Bitter) Mione & Bye	Mexico	GU256348
		J. chotanae S. Leiva & Mione	Peru	GU256327
		J. contumacensis S. Leiva & Mione	Peru	GU256309
		J. darcyana Mione	Costa Rica	GU256356
		J. dendroidea S. Leiva & Mione	Peru	GU256315
		J. dentata (Ruiz & Pavón) Benítez	Peru	GU256292
		J. grandiflora (Robinson & Greenman) D´Arcy, Mione & Davis	Mexico	GU256350
		J. guillermoguerrae Mione & S. Leiva	Peru	GU256314
		J. herrerae (C.V. Morton) Mione	Bolivia	GU256321
		J. lanata S. Leiva & Mione	Peru	GU256328
		J. leivae Mione	Peru	GU256310
		J. lezamae S. Leiva & Mione	Peru	GU256306
		J. lojae Mione	Ecuador	GU256329
		J. lomana Mione & S. Leiva	Peru	GU256297
		J. mionei S. Leiva & Quipuscoa	Peru	GU256296
		J. nigricolor S. Leiva & Mione	Peru	GU256325
		J. oppositifolia S. Leiva & Mione	Peru	GU256337
		J. paneroi Mione & S. Leiva	Peru	GU256326
		J. procumbens (Cav.) J.L. Gentry.	Costa Rica	GU256339
		J. procumbens (Cav.) J.L. Gentry.	Mexico	GU256343
		J. repandidentata (Dunal) Hunz.	Costa Rica	GU256353
		J. repandidentata (Dunal) Hunz.	Mexico	GU256352
		J. repandidentata (Dunal) Hunz.	Nicaragua	GU256351
		J. sagastegui Mione	Peru	GU256331
		J. salpoensis S. Leiva & Mione	Peru	GU256336
		J. sanchezvegae S. Leiva & Mione	Peru	GU256318
		J. sinuosa (Miers) Mione	Peru	GU256305
		J. tayabambae S. Leiva & Mione	Peru	GU256316
		J. truxillana S. Leiva & Mione	Peru	GU256295
		J. umbellata (Ruiz & Pavón) Mione	Peru	GU256291
		J. ventricosa (Baker) Mione	Peru	GU256317
		J. viridiflora (Humb., Bonpl. & Kunth) M. Nee & Mione	Ecuador	GU256312
		J. weberbaueri (Dammer) Mione	Peru	GU256324
		J. yacheri Mione & S. Leiva	Peru	GU256323
		J. yungayensis Mione & S. Leiva	Peru	GU256313
		Jaltomata sp. RJM 2010	Mexico	GU256345

Sequences were downloaded from National Center for Biotechnology Information (NCBI): https://www.ncbi.nlm.nih.gov/)

Species delimitation

The homoplasy index test was performed with Splitstree version 4.17.0 (Huson & Bryant 2006). This test focuses on detecting recombination between sister clades with new lineages (Fuentes-Aragón *et al*. 2020), where a value greater than 0.05 is indicative of a new species, indicating no recombination (Bruen *et al*. 2006). Split decomposition, LogDet functions were used to calculate the proportion of sites assumed to be invariant, and the pairwise homoplasy index was calculated with the PHI test for recombination.

Determination of total soluble solids (TSS %)

The determination of TSS % was carried out according to the Association of Official Analytical Chemists methodology (AOAC 1995). Ten g of fresh fruit were ground, and two drops of the juice obtained were placed in a digital refractometer. The value is reported as a percentage.

Determination of titratable acidity (TA %)

The determination of TA % was carried out according to the Association of Official Analytical Chemists methodology (AOAC 1995). Ten g of fruit were ground with 50 mL of distilled water. The total volume was obtained, then an aliquot of 5 mL was taken, and 3 drops of phenolphthalein were added as an indicator and titrated with 0.1 N NaOH. Values are reported as percentage of citric acid.

$$Titratable\ acidity\,(\%) = \frac{mL\ NaOH \times N\ NaOH \times meq \times VT \times 100}{A \times g}$$ was used:

Where: mL NaOH = millilitres of sodium hydroxide spent in the titration; N NaOH = normality of sodium hydroxide; meq = milliequivalents of citric acid (0.064); VT = volume of sample prepared; A = aliquot taken for measurement; g = weighed grams of fruit.

Calculation of the TSS/TA ratio was determined by dividing the total soluble solids content (TSS %) by the percentage of titratable acidity (TA %).

Results

The dataset was 47 sequences of *Jaltomata* species and *Nicotiana tabacum* as outgroup. For Jpd a sequence length of 820 bases was obtained. The evolutionary model was HKY + Γ+ I, with invariant sites and gamma distribution. The consensus tree was obtained with MrBayes and 20,002 trees were generated, with a standard deviation of 0.0042, from which 15,002 trees were analysed to calculate the Bayesian posterior probability. From the maximum likelihood analysis, bootstrap supports greater than 71% are shown.

Phylogenetic tree of the genus Jaltomata

Specimen Jpd, the target of this study, was separated from the *J. procumbens* group, with a posterior probability of 100%, and bootstrap support of 88% (Fig. 1). This specimen, Jpd, was grouped together with the taxon *Jaltomata* sp. RJM 2010 (GU256345), with a posterior probability and bootstrap support of 100 and 87%, respectively. This is not expected, suggesting that it would correspond to a new species, with *J. bohsiana* as the closest sister species of the clade.

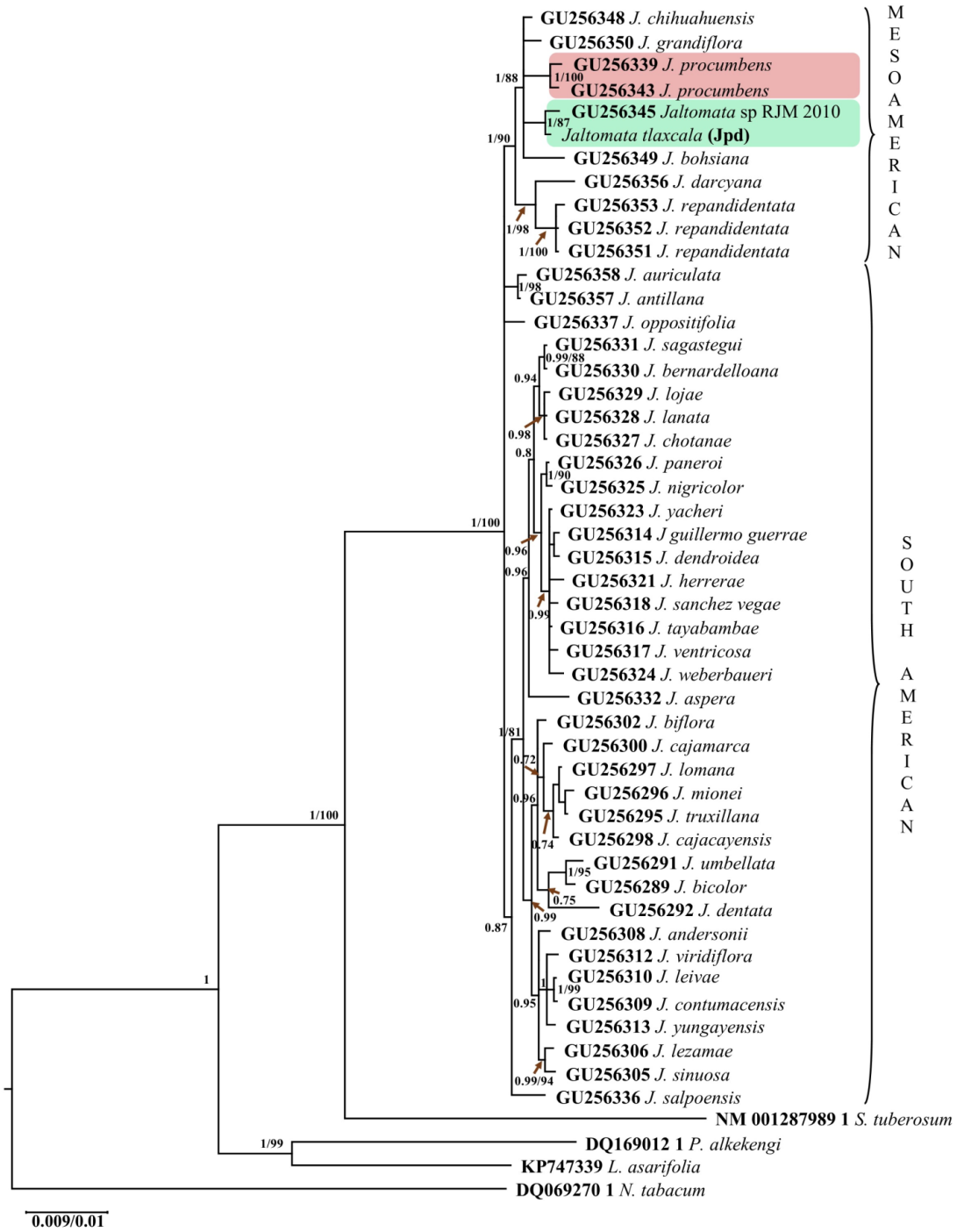

FIGURE 1. Phylogenetic tree of the genus *Jaltomata*, depicting Mesoamerican and South American clades, with *J. procumbens* decumbent (Jpd), object of study in this work, and renamed as *J. tlaxcala*, showing *Nicotiana tabacum* as outgroup. Statistical support represented with posterior probability/boostrap support.

Species delimitation

In species delimitation, the pairwise homoplasy index indicated no evidence of genetic recombination with a value of PHI = 1.0 (Fig. 2).

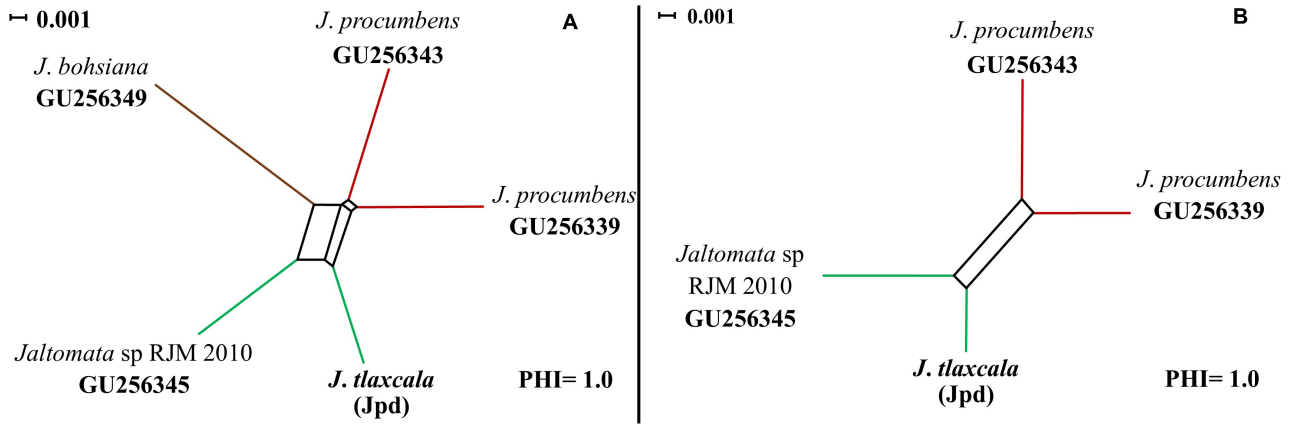

FIGURE 2. Species delimitation: A: *J. procumbens* decumbent (Jpd) group, renamed as *J. tlaxcala*vs. *J. procumbens* group with *J. bohsiana*; B: *J. procumbens* decumbent (Jpd) group, renamed as *J. tlaxcala* vs. *J. procumbens* group. The value of PHI = 1.0 means that there is no genetic recombination.

Taxonomy

Jaltomata tlaxcala Flores-Sánchez & Sandoval-Villa *sp. nov.* (Figures 3–6).
The sequence of the specimen was deposited in GenBank under accession number PP272016.

Holotype: Mexico, Tlaxcala, municipality of Ixtenco, growing on the side of maize crop field, 19°15′ N and 97°53′ W, predominant temperate sub-humid climate C(w1) and C(w2), elevation 2500 m.a.s.l., August 11th, 2015.

Diagnosis: *Jaltomata tlaxcala* differs from *J. procumbens* and *J. bohsiana* (Table 3) in growth habit, prostrate or decumbent (*J. tlaxcala*) vs. erect (*J. procumbens* and *J. bohsiana*), leaf type, subalternates (*J. tlaxcala*) vs. alternate (*J. procumbens* and *J. bohsiana*), number of flowers per inflorescence, 2 to 3 flowers (*J. tlaxcala*) vs. up to 18 flowers (*J. procumbens*) and 5 to 7 flowers (*J. bohsiana*), pedicel type, subterete or almost terete (*J. tlaxcala*) vs. pedicel with longitudinal elevated ridges (*J. procumbens*) and angled pedicel (*J. bohsiana*), calyx characteristics and position in the fruit, calyx marcescent green and covering about half of the fruit with the tips of the lobes raised (*J. tlaxcala*) vs. calyx green or green with purple colour, plane to reflexed and showing the fruit on lateral view or bowl-like on the fruit (*J. procumbens*), and calyx purple, recurved and concave in transverse section (*J. bohsiana*), corolla colour, pale yellow and dark green flower base, giving the overall appearance of a ring (*J. tlaxcala*) vs. pale green, light green (*J. procumbens*) and pale green (*J. bohsiana*), stigma shape, discoid (*J. tlaxcala*) vs. capitate (*J. procumbens* and *J. bohsiana*), fruit colour, pale green with few dark green or purple vertical lines, with a slight purple spot on one side of the fruit when ripe (*J. tlaxcala*) vs. black or dark purple when ripe (*J. procumbens*) and dark bright when ripe (*J. bohsiana*), seed shape and measurements, oblate form with length of 1.68 mm, width of 1.51 mm and thickness of 0.51 mm (*J. tlaxcala*) vs. ovate to reniform with length of 1.46 mm, width of 1.29 mm and thickness of 0.52 mm (*J. procumbens*) and ovate to sub-triangle with length of 1.30 mm, width of 0.98 mm and thickness of 0.38 mm (*J. bohsiana*).

Description

Growth habit: herbaceous, decumbent plant, 33.7 to 46.5 cm high (Fig. 3A). Axillary buds (Figs. 3B–C). Leaves 62.92 to 95.57 mm long, simple, subalternate, ovate to elliptic, attenuate base with slightly winged petioles, 7.86–27.28 mm long and 1.05–5.68 mm wide, margin sinuate, apex acuminate, without stipules (Figs. 3D–F).

Inflorescence: umbel of two to three flowers (Figs. 3G–H).

Flower: perfect actinomorphic flower, pale yellow corolla lobes and dark green flower base, giving the overall appearance of a ring, transparent whitish nectar droplets at the base of the stamens (Figs. 3I–K).

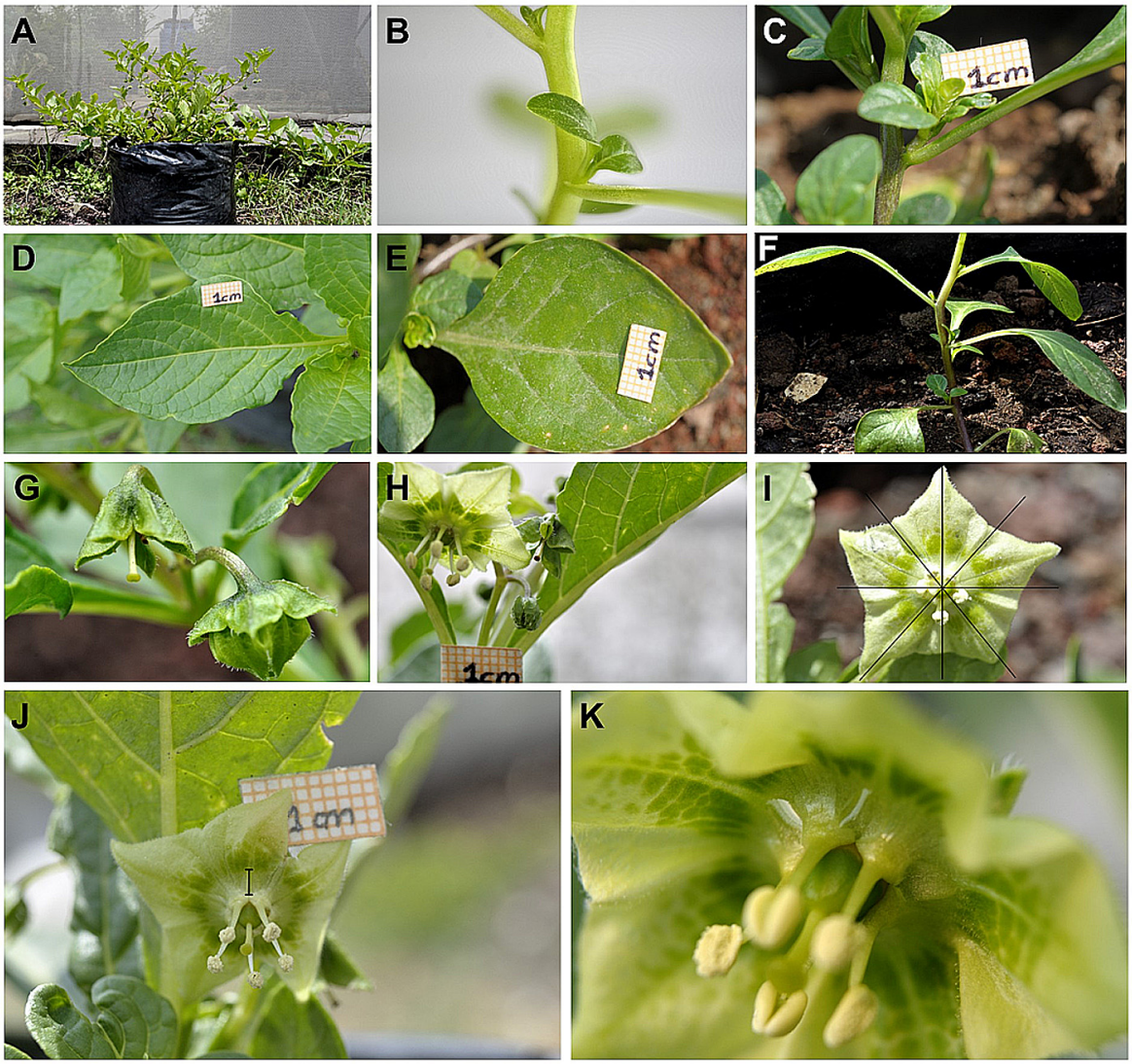

FIGURE 3. Vegetative and reproductive morphology of *J. tlaxcala*. A: prostrate/decumbent habit; B–C: axillary buds; D–F: subalternate leaf arrangement, ovate to elliptic; G–H: umbel of two to three flowers; I–K: perfect actinomorphic flower.

Anthesis: process of flower opening lasting 3 days, at the beginning of the third day with the corolla fully open the anthers approach the stigma (Figs. 4L–N). Pedicel and perianth: pedicel subterete or almost terete, pubescent in early flower bud stage and decreases in late stage, becoming light or sparse (Fig. 4O); perianth rotated, gamosepalous and gamopetalous (Fig. 4P). Calyx: pubescence present, with the same behaviour as pedicel pubescence, actinomorphic, gamosepalous, 5 lobes pyramidal in shape, 12 mm diameter, lobe length 4.87 to 5.76 mm and sinus length 2.18 to 2.82 mm, lobe:sinus ratio 1.76 to 2.27; calyx marcescent green, at the base purple, in fruiting the lobes yellow, and gradually disappears the purple colouration of the base present in flowering, yellow in the fall or senescence of the fruit; in ripe fruit, the calyx is light green and increases in size the yellow border on the lobes, once the fruit is detached the calyx remains on the plant and takes on a light green to yellow colouring; at fruiting stage, the calyx covers about half of the fruit with the tips of the lobes raised, at maximum fruit size the calyx covers the upper part of the fruit (Figs. 4Q–S). Corolla: actinomorphic, gamopetalous, 5 pyramidal lobes with lobe length 8.9 to 11.7 mm and sinus length 4.6 to 6.5 mm, with a lobe:sinus ratio of 1.7 to 2.1; pubescent from bud (Fig. 4T & 5U).

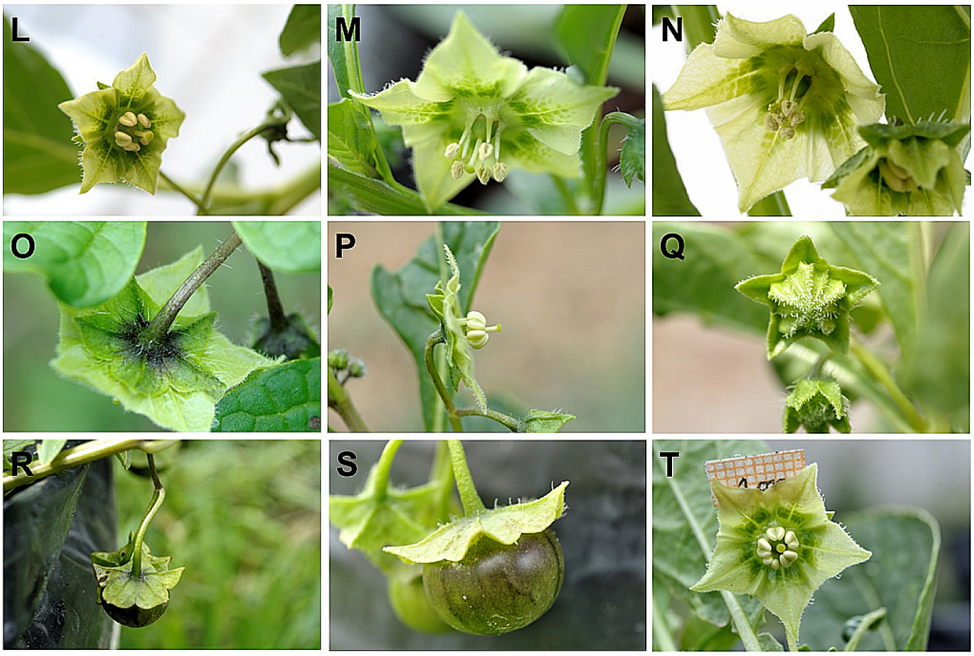

FIGURE 4. Anthesis and floral morphology of *J. tlaxcala*. L–N: anthesis; O–P: pedicel subterete or almost terete and perianth rotated, gamosepalous, gamopetalous; Q–S: calyx pubescence, actinomorphic, gamosepalous; T: corolla actinomorphic, gamopetalous.

Androecium: antisepalous, stamens alternate with corolla lobes, hypogynous, stamen 5.48 to 7.09 mm long and 0.29 to 0.51 mm wide, anthers bilocular and distichous, parallel, 1.5 to 2.2 mm long and 0.97 to 1.22 mm wide (Figs. 5V–X).

Gynoecium: bilocular, compound, placentation parietal, ovary superior, stigma discoid, 0.28 to 0.63 mm wide and 0.34 to 0.66 mm long, style apical, 0.17 to 0.36 mm in diameter and 2.85 to 3.79 mm long, pre-flowering alternate (Figs. 5Y–Z).

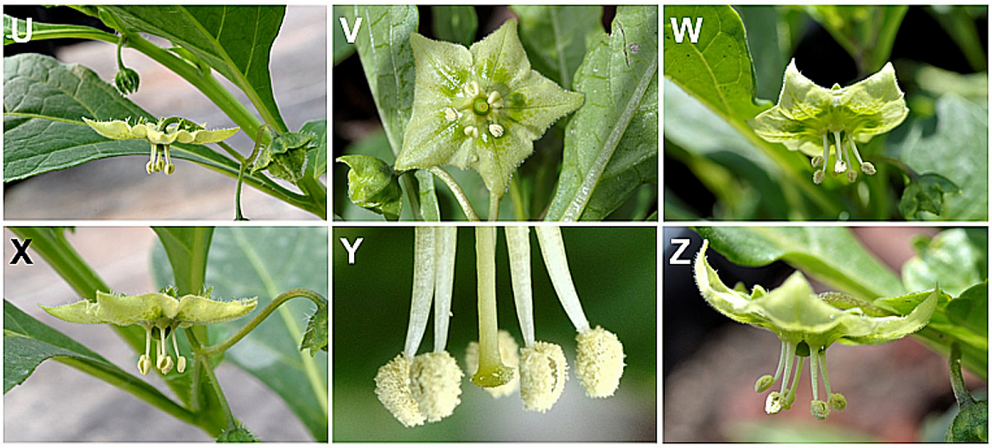

FIGURE 5. Androecium and gynoecium morphology of *J. tlaxcala*. U: corolla actinomorphic, gamopetalous; V–X: androecium antisepalous, hypogynous; Y–Z: gynoecium bilocular, ovary superior, stigma discoid.

Fruit: a berry, pale green when ripe, with few dark green or purple vertical lines, with a slight purple spot on one side of the fruit, fruit length and width 11.9–15 and 11.8–14.7 mm, respectively, and equatorial diameter 9.5–11.3 mm (Figs. 6CC–EE).

Seed: 36 to 162 seeds oblate, albuminous, dicotyledonous embryo; length, width and thickness of seed 1.68, 1.51 and 0.51 mm, respectively (Figs. 6GG–HH).

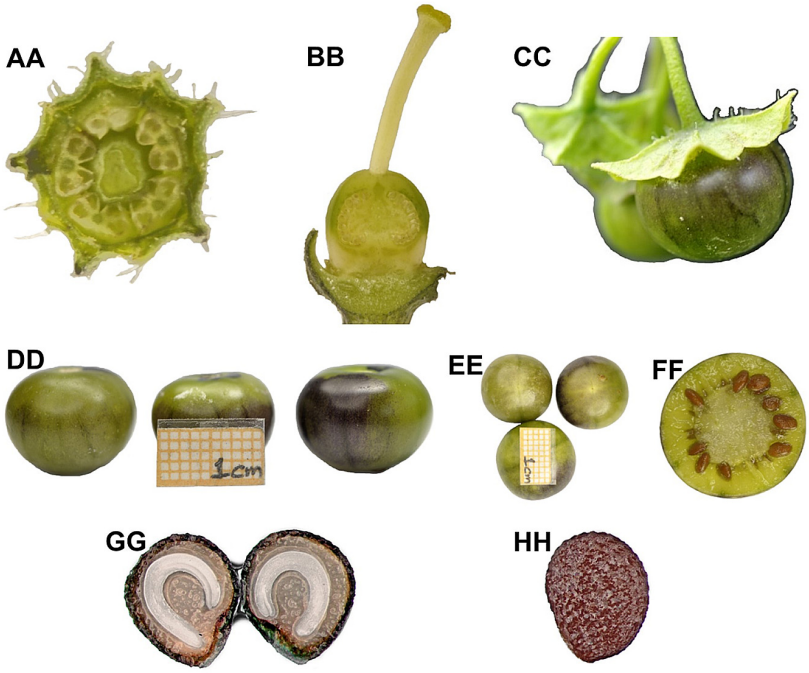

FIGURE 6. Reproductive morphology of *J. tlaxcala* fruits and seeds. AA–BB: gynoecium bilocular, ovary superior, stigma discoid; CC–FF: fruit a berry; GG–HH: seed oblate, albuminous, dicotyledonous embryo.

Discussion

The genus *Jaltomata* is rapidly evolving, with extensive diversity in flower shape and size, nectar and fruit colour (Wu *et al*. 2019). The species that comprise it encompass a wide geographic, morphological, physiological, reproductive form and biochemical variation (Haak *et al*. 2014). This condition makes it difficult to distinguish them (Mione & Bye 1996), especially when only dried specimens are studied, which leads to gaps in information on floristic knowledge, and molecular studies have been implemented to help resolve this situation (Mione *et al*. 1994).

In the first molecular phylogeny study on the genus by Mione *et al*. (1994), where chloroplast DNA restriction sites were used, two clades were identified, the South and Mesoamerican; in the former, specimens are distinguished by being sub-shrubs or shrubs, with a rotated, campanulate or tubular corolla, and red or orange fruits; in the latter, by being herbaceous, with a rotated corolla and purple or black fruits. In addition, this study for the Mesoamerican clade includes a semi-domesticated, green-fruited form tentatively assigned to *J. procumbens*, which is grouped with *J. procumbens*, *J. repandidentata*, and *J. conspersa*, with a sister group consisting of *J. oaxaca* and an accession of *J. conspersa*.

In a second study, Miller *et al*. (2011), using more species (50 accessions including 8 new unnamed specimens) and the waxy gene (GBSSI), include three collections of green fruit, two of South American and one Mesoamerican origin. The green-fruited specimen identified as *Jaltomata* green fruit (GU256345), Mesoamerican and from Mexico, was separated from the *J. procumbens* clade, with the species *J. bohsiana* located between the two groups. A similar condition to that presented in this work (Fig. 1), where *Jaltomata* green fruit corresponding to GU256345 *Jaltomata* sp. RJM 2010, was grouped with the specimen under study Jpd, renamed as *J. tlaxcala*, and *J. bohsiana* was placed as the closest sister species of the clade.

However, the aforementioned works (Miller *et al*. 2011; Mione *et al*. 1994) were aimed at studying phylogenetic relationships within the genus *Jaltomata*, and not at delimiting new species. This could explain why green-fruited specimens are considered as races or, for the Mesoamerican origin, as part of *J. procumbens*. The green fruit characteristic is thought to have evolved at least three times independently, within the red or orange and purple or black fruit lineages, a characteristic that is considered a case of neoteny, as the fruit retains its green colour when ripe (Miller *et al*. 2011). This type of evolutionary change can lead to a new species if this characteristic represents a selective advantage under certain conditions (Box & Glover 2010).

It is worth mentioning that Jpd (*J. tlaxcala*), considered semi-domesticated and closely linked to the traditionally managed agro-ecosystem, is more appreciated for its more palatable fruits, because they are sweeter and almost never acidic, compared to the purple or black fruits of *J. procumbens* (Williams 1985). This characteristic is mainly due to the palatability of the fruit, where high palatability values are important in determining consumer acceptance of a product (Santacruz-Oviedo *et al*. 2018). Palatability is determined by the ratio of total soluble solids (reference index used to quantify the number of soluble sugars) (Scalisi & O'Connell 2021) and titratable acidity (TA). High values of this ratio, respond to higher percentages of total soluble solids (TSS) and lower TA, behaviour reported in species such as *Fragaria* × *ananassa* (Santacruz-Oviedo *et al.* 2018) and *Vaccinium* spp. (Medeiros *et al*. 2017) for which TSS/TA ratio values of up to 54.83 and 20.57, respectively, were reported. The fruits of Jpd (*J. tlaxcala*) showed a similar behaviour with a TSS/TA ratio of up to 56.25, with averages of TSS percentages of 10.27% and TA of 0.21% (data not shown). This characteristic could favour the selection preference, its tolerance and sponsorship within the cultivation fields, and the permanence of the genotype in a specific niche, until it differentiates from *J. procumbens*; a process that occurs over time, as a result of the association between a plant specimen and human activities (Davis & Bye 1981).

The homoplasy index, which allows determining the level of recombination between closely related organisms phylogenetically, assessing species boundaries and indicating their evolutionary independence (Xu *et al*. 2022; Quaedvlieg *et al.* 2014), indicated that there is no evidence of genetic recombination, with a value of PHI = 1.0 (Fig. 2), which supports the results obtained in the phylogenetic tree (Fig. 1).The differences between Jpd, *J. procumbens*, and *J. bohsiana* are shown in Table 3.

TABLE 3. Main differences between characteristics of the species *Jaltomata procumbens*, *J. bohsiana* and *J. tlaxcala*, former *J. procumbens* decumbent (Jpd).

Characteristics	**Specimens**		
	***J. procumbens* (Cav.) J.L. Gentry (Mione, pers. comm. 2019)**	***J. bohsiana* (Mione & D.M. Spooner)**	***J. tlaxcala***
Height and growth habit	Herbaceous, erect to procumbent of up to 1.8 m height.	Erect of 0.6 to 0.9 m height.	Prostrate or decumbent of 0.34 to 0.47 m height.
Leaf	Alternate, margin entire to dentate, winged petioles of up to 4.5 cm.	Alternate, margin entire to slightly undulate of up to 3.3 cm.	Subalternates, margin sinuate, of 6.3 to 9.6 cm long, slightly winged petioles of 0.79–2.7 cm long.
Inflorescence	To 18 flowers	Of 5 to 7 flowers	Of 2 to 3 flowers
Pedicel	Pedicel with longitudinal elevated ridges	Angled pedicel	Subterete or almost terete
Calyx	In flowering the main veins of the abaxial face, with green or green with purple colour; in ripe fruit green to purple, plane to reflexed and showing the fruit on lateral view, or bowl-like on the fruit, partially hiding the fruit on lateral view.	Recurved and concave in transverse section, purple, and dark on the top of lobes on upper surface.	Calyx marcescent green, at the base purple, in fruiting the lobes yellow, and gradually disappears the purple colour of the base present in flowering, yellow in the fall or senescence of the fruit; in ripe fruit, the calyx is light green and increases in size with a yellow border on the lobes, once the fruit is detached the calyx remains on the plant and takes on a light green to yellow colouring. At fruiting stage, the calyx covers about half of the fruit with the tips of the lobes raised, at maximum fruit size the calyx covers the upper part of the fruit.
Corolla	Pale green, light green	Pale green	Pale yellow and dark green flower base, giving the overall appearance of a ring.
Androecium	Stamens of 4.5 to 7 mm length. Anthers of 1.6 to 2.8 mm length.	Stamens of 3 to 7 mm length. Anthers of 1.7 to 2 mm length.	Stamens of 5.48 to 7.09 mm. Anthers of 1.5 to 2.2 mm length.
Gynoecium	Stigma capitate.	Stigma capitate.	Stigma discoid.
Fruit	Black or dark purple colour when ripe. 9.7 × 17 mm size.	Dark bright colour when ripe. 6 × 8–9 × 11 mm size when fresh.	Pale green when ripe, with few dark green or purple vertical lines, with a slight purple spot on one side of the fruit. 11.9–15.0 × 11.8–14.7 × 9.5–11.3 mm size.
Seed	Ovate to reniform. With 4 to 198 seeds, length, width and thickness of seed 1.46, 1.29, and 0.52 mm, respectively.	Ovate to sub-triangle, alveolate. Numerous seeds, length, width and thickness of seed 1.30, 0.98, and 0.38 mm, respectively.	Oblate form. With 36 to 162 seeds, length, width and thickness of seed 1.68, 1.51, and 0.51 mm, respectively.

Considering the differences in the characteristics between *J. tlaxcala*, former *J. procumbens* (Jpd), *J. procumbens*, and *J. bohsiana* (Table 3), along with the result obtained in the pairwise homoplasy index (PHI = 1.0) (Fig. 2) and the phylogenetic tree with posterior probability and boostrap support values (Fig. 1), it is proposed that *J. tlaxcala* should be recognised as a different taxon from *J. procumbens* and that the name should be established as *Jaltomata tlaxcala* Flores-Sanchez & Sandoval-Villa *sp. nov*.

Conclusion

DNA sequencing and the phylogenetic trees allowed us to define the taxonomic status of the specimen named in this work as *Jaltomata procumbens* decumbent, tentatively assigned to the species *Jaltomata procumbens*. *Jaltomata procumbens* decumbent differed from *Jaltomata procumbens* in growth habit, number of flowers, type of leaves, pedicel and calyx, corolla colour, anther length, fruit colour, stigma, and seed characteristics. Based on the results obtained in this work, the specimen under study demonstrated clear differences in the molecular approach, as well as in morphological features from other previously reported species.

Key to the species of *Jaltomata* of Mexico (based on Mione & Spooner 2010)

1a. Anthers unequal in size, most noticeable during the pistillate phase while anthers are undehisced; filaments sigmoid or curved during hermaphroditic phase; style curved; habitat in coffee plantations and roadsides ..... *J. repandidentata*
1b. Anthers equal in size; filaments straight during hermaphroditic phase; style straight; habitat variable, including agricultural fields and other disturbed areas 2
2a. Calyx lobes concave in cross section; calyx purple at time of flowering, < 6.8 mm diam ..... *J. bohsiana*
2b. Calyx lobes plane to reflexed in cross section; calyx mostly green at time of flowering, >7 mm diam 3
3a. Anthers longer than 2.8 mm; leaves and branches densely velutinous ..... *J. grandiflora*
3b. Anthers shorter than 2.8 mm; leaves and branches glabrate to pubescent or hirsute 4
4a. Vestiture of stems and leaves variable (including glabrate) but never hirsute; habit erect; corolla 5-lobed or with alternating lobes and lobules totaling 10; flowers per inflorescence up to 18 flowers; colour of fruit black or dark purple when ripe; Arizona, United States, to Ecuador ..... *J. procumbens*
4b. Vestiture of stems and leaves glabrate to hirsute; habit prostrate or decumbent; colour of fruit black or green when ripe; corolla 5-lobed; flowers per inflorescence less than 5 5
5a. Stems and leaves hirsute; habit prostrate; corolla pale green, 5 attenuate lobes; inflorescence up to 4-flowered; obtuse or obtuse-acuminatecalyx; plants with fruit colour purple or green when ripe; northern Mexico ..... *J. chihuahuensis*
5b. Leaves glabrate and vestiture of stems variable (including glabrate) but never hirsute; habit prostrate or decumbent; corolla pale yellow, and dark green flower base with a ring appearance, 5 pyramidal lobes; inflorescence up to 3-flowered; pyramidal-shaped calyx; pale green fruit with few dark green or purple vertical lines when ripe, with a slight purple spot on one side of the fruit; associated with agricultural fields; Central Highland Valley of Mexico ..... *J. tlaxcala*

Declaration of conflicting interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this manuscript.

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