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Morphological variation in *Bessera* (Asparagaceae: Brodiaeoideae) allows for the recognition of two new species

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Abstract

Bessera (Asparagaceae: Brodiaeoideae) is a genus endemic to Mexico. It currently has two described species: *B. elegans* with a wide geographic distribution from Durango and Sinaloa in the Sierra Madre Occidental, across the Transmexican Volcanic Belt to Oaxaca in the Sierra Madre del Sur, and *B. tuitensis* which is endemic to the Sierra del Cuale in Jalisco. Most of the morphological variation in *Bessera* occurs in western Mexico. We measured ten morphological characters for 280 plants from 21 populations, including *B. tuitensis*, to answer the following questions: Can Moore's Group B of *B. elegans* be recognized as a different species? Are the newly included *B. elegans s. l.* populations from Colima different from *B. elegans s. str.*, and from *B. elegans s. l.* (Moore's group B)? Is there a significant relationship between morphological variation and climate variables for these species? The statistical analyses (ANOVA, MANOVA, and discriminant analysis) allowed us to recognize two new *Bessera* species, described here as *B. elegantissima* and *B. ramirezii*. Additionally, we provide a morphological key for *Bessera*, illustrations, a distribution map, and photographs of all the species.

Keywords: endemic species, geophytes, Pacific Lowlands, tropical forest, western Mexico

Introduction

Bessera Schultes f. (1829: 121) is a genus of perennial geophytes endemic to Mexico, which belongs to the Milla clade of the subfamily Brodiaeoideae (Asparagaceae). Brodiaeoideae has 14 recognized genera and is distributed in western North America (Fay & Chase 1996, Pires *et al.* 2001, Pires & Sytsma 2002, Chase *et al.* 2009, Gándara *et al.* 2009, 2014, Gutiérrez & Terrazas 2020). Brodiaeoideae is a monophyletic subfamily divided into three main clades. The first of these clades includes the genera *Brodiaea* Smith (1811: 2), *Dichelostemma* Kunth (1843: 469) and *Triteleiopsis* Hoover (1941: 98), and is distributed in California, the Pacific Northwest, western North America and the Sonoran Desert (Pires & Sytsma 2002). The second clade corresponds to the genus *Milla* Cavanilles (1793: 76), which is endemic to Mega-Mexico 3 *sensu* Rzedowski (1993). The third clade includes *Triteleia* Douglas ex Lindley (1829: 1293), *Bloomeria* Kellogg (1863: 11) and *Muilla clevelandii* (Watson 1885: 379) Hoover (1955: 23), which are distributed in the Pacific Northwest, from California to Arizona and on the Great Plains (Pires & Sytsma 2002).

The systematics of the Milla clade is complicated. It is composed of seven genera: *Behria* Greene (1886: 143), *Bessera*, *Dandya* Moore (1953: 266), *Jaimehintonia* Turner (1993: 86), *Milla*, *Petronymphe* Moore (1951: 258), and *Xochiquetzallia* J.Gut. in Gutiérrez & Terrazas (2020: 42) (Pires *et al.* 2001, Pires & Sytsma 2002, Gándara *et al.*

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2009, 2014, Gutiérrez *et al.* 2010, Gutiérrez & Terrazas 2020). *Behria* is a monotypic genus distributed in the southern Baja California Peninsula (Gándara *et al.* 2009, 2014). *Bessera* has two species and a wide distribution range along the Sierra Madre Occidental, the Transmexican Volcanic Belt, the Balsas Basin, the Sierra Madre del Sur, and the Pacific Lowlands (Gándara *et al.* 2009, 2014, Gutiérrez *et al.* 2017). The distribution of *Dandya* and *Jaimehintonia* is restricted to the Chihuahuan Desert. *Milla* consists of ten described species and has the widest geographic distribution, which spans the Sierra Madre Occidental, the Sierra Madre del Sur, the Transmexican Volcanic Belt, the Balsas Basin, the Chihuahuan Desert, and the Baja Californian provinces. With two and three species respectively, *Petronymphe* and *Xochiquetzallia* are endemic to the Sierra Madre del Sur in the Balsas Basin (Gándara *et al.* 2009, 2014, Gutiérrez *et al.* 2017, Gutiérrez & Terrazas 2020).

Recent molecular phylogenetic studies of the Milla clade state that *Xochiquetzallia* is the sister genus to all the other genera, then *Dandya*, *Milla* and *Jaimehintonia* form a grade. Finally, *Petronymphe* is sister to the clade formed by the sister taxa *Behria* and *Bessera* (Gándara *et al.* 2014, Gutiérrez *et al.* 2017). *Behria* is considered by Gándara *et al.* (2009, 2014) and Gutiérrez *et al.* (2010, 2015) to be a valid genus based on morphological and molecular evidence. Later, Gutiérrez *et al.* (2017) identified *Behria tenuiflora* as a part of *Bessera*. Here, we recognize them as separate genera based on morphological and geographic evidence.

Currently, *Bessera* encompasses two described species, *B. elegans* Schultes f. (1829: 121) and *B. tuitensis* Ramírez-Delgadillo (1992: 131). Moore (1953) recognized three groups: Group A, with *B. elegans* (hereafter, *B. elegans s. str.*) and groups B and C (hereafter, *B. elegans s. l.*).

B. elegans s. str. has the widest geographic distribution, from Sinaloa and Durango in the Sierra Madre Occidental, the southern part of the Chihuahuan Desert, and across the Transmexican Volcanic Belt to the Sierra Madre del Sur in Oaxaca and the Balsas Basin. Moore (1953) mentioned that the type locality of *B. elegans* is in Sultepec at Mexico state. The populations of this group grow mainly in oak forest and share their limits with tropical dry forest from 900 to 2175 m a.s.l. According to Moore (1953), Group A (*B. elegans s. str.*) has the following characteristics: stout leaves and scapes, umbels up to 30 flowers, pedicels 2–6(–10) cm long, perianth 5–10(–13) mm long, the tepals lobes are one and a half to two (rarely one) or more times as long as the perianth, the stamens are mostly prominently exserted with a generally dentate staminal tube, with violaceous or red filaments and with anthers 2 mm long or more when dry.

Bessera elegans s. l. is distributed along the Pacific Lowlands province, from Sinaloa to Oaxaca. The populations of this group grow in savanna-like vegetation *sensu* Rzedowski (1978), subdeciduous tropical forest, and tropical dry forest, from almost sea level (10 m) up to 1100 m a.s.l. Group B has generally slender leaves and scapes, 2–8 flowers per umbel, pedicels 2–5 cm long, often pale on drying with a bluish or purplish cast and noted as varying from red or pink to purple in the wild, the perianth is 10–15 mm long, gradually enlarges upward and generally equaling or exceeding the body of the ovary in length, the tepals lobes are 10–14 mm long, shorter than to equaling or slightly exceeding the tube in length, the stamens are generally less prominently exserted usually with an edentate staminal tube, pale violaceous filaments and anthers 1–1.5(–2) mm long (Moore 1953). Moore (1953) mentioned Group C, similar to Group B, from a single locality in Punta de Mita, Nayarit.

Bessera tuitensis is endemic to the Sierra de El Cuale, Jalisco at the northern part of the Sierra Madre del Sur mountains. The populations grow in oak-pine forest and savanna-like vegetation, from 700 to 900 m a.s.l. This species has slender leaves and scapes, (6–)13–28(–34) flowers per umbel, pedicels (2.5–)3–4(–5.5) cm long, the perianth is 1.5–2(–2.5) cm, the tepals lobes are (0.9–)1–1.1(–1.5) cm, the stamens are edentate and not exserted, the filaments are 1–1.1(–1.5) cm, are connate at base forming a staminal ring, and the anthers (1.1–)1.5(–2) cm (Ramírez-Delgadillo 1992).

Due to most of the morphological variation of *Bessera* being concentrated in western Mexico, we studied 280 plants from 21 populations to answer the following questions: 1) Can Moore's Group B of *Bessera elegans* be recognized as a different species? 2) Are the newly included *B. elegans s. l*. populations from Colima different from *B. elegans s. str*. and from *B. elegans s. l.* (Moore's Group B)? 3) Is there a significant relationship between morphological and climate variables for these species?

Materials and methods

Taxon sampling

We measured 280 plants from 21 populations of *Bessera*. For *Bessera elegans s. str*. (Moore's Group A) we included 15 populations and two of *B. elegans s. l.* (Moore's Group B). In addition, two populations not studied by Moore (1953) of

B. elegans s. l. from the state of Colima, and two of *B. tuitensis* described by Ramírez-Delgadillo (1992) were included in the analysis. Lastly, Moore (1953) identified a third group (C) of *B. elegans*, but we could not find any of these plants (Table 1, Fig. 1). Voucher specimens were deposited in the IBUG Herbarium (acronyms follow Thiers 2020). Field trips were carried out from July to October 2020, covering the central western states in Mexico (Aguascalientes, Colima, Jalisco, Nayarit and Zacatecas) where most of the morphological variation has been documented (Moore 1953, Ramírez-Delgadillo 1992, Gándara *et al.* 2009) (Table 1).

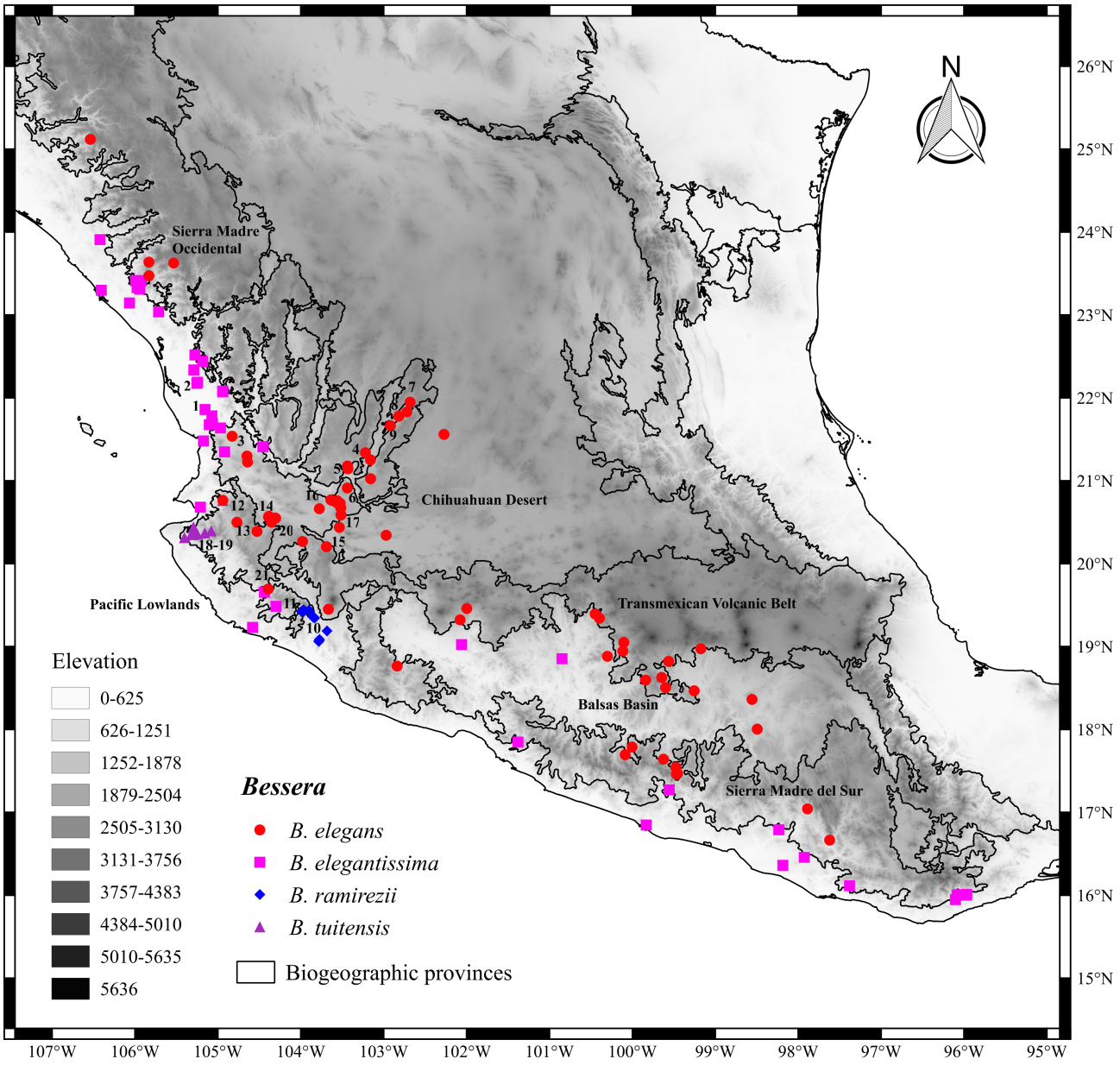

FIGURE 1. Geographic distribution of the genus *Bessera*. Red circles = *B. elegans*, fuchsia squares = *B. elegantissima*, blue rhombuses = *B. ramirezii*, and lilac triangles = *B. tuitensis*.

Morphological characters

Ten quantitative characters were selected based on the taxonomic revision of *Bessera* by Moore (1953) and in the description of *B. tuitensis* by Ramírez Delgadillo (1992) (Table 2). Measurements were taken *in situ* on live plants using an electronic vernier (Absolute AOS Digimatic, Mitutoyo ®), and a metric scale. We measured one flower per plant, trying to measure at least 15 flowers per population from different plants. All the flowers were measured directly on living plants. Some flowers were dissected and photographed for comparisons.

TABLE 1. Georeferenced data for *Bessera* populations measured. Specimens deposited in the IBUG herbarium (acronym based on Thiers 2020).

Population	Species	Longitude	Latitude	Elevation m a.s.l.	Voucher
1	*B. elegans s. l.*	-105.155376	21.859633	73	*E. Ruiz & E. Gándara 654*
2	*B. elegans s. l.*	-105.245421	22.188473	18	*E. Ruiz & E. Gándara 655*
3	*B. elegans s. str.*	-104.828628	21.537225	934	*E. Ruiz & E. Gándara 661*
4	*B. elegans s. str.*	-103.431351	21.144445	1357	*E. Ruiz & E. Gándara 663*
5	*B. elegans s. str.*	-103.436707	21.177858	1754	*E. Ruiz & E. Gándara 664*
6	*B. elegans s. str.*	-103.438649	20.912988	1499	*E. Ruiz & E. Gándara 665*
7	*B. elegans s. str.*	-102.68263	21.94846	1796	*E. Ruiz & E. Gándara 666*
8	*B. elegans s. str.*	-102.919505	21.665275	1582	*E. Ruiz & E. Gándara 669*
9	*B. elegans s. str.*	-103.16044	21.25234	1186	*E. Gándara & E. Ruiz 3256*
10	*B. elegans s. l.*	-103.8330556	19.3452778	1049	*J. P. Brunel et al. 828*
11	*B. elegans s. l.*	-103.9675	19.4244444	1049	*E. Gándara et al. 3262*
12	*B. elegans s. str.*	-104.9405833	20.7627778	1016	*E. Gándara et al. 3263*
13	*B. elegans s. str.*	-104.7705556	20.4997222	1400	*E. Gándara et al. 3264*
14	*B. elegans s. str.*	-104.3858333	20.5713889	1488	*E. Gándara et al. 3266*
15	*B. elegans s. str.*	-103.6905556	20.2038889	2175	*E. Gándara et al. 3267*
16	*B. elegans s. str.*	-103.6380556	20.7691667	1540	*E. Gándara et al. 3274*
17	*B. elegans s. str.*	-103.5247996	20.7270027	1722	*E. Gándara et al. 3275*
18	*B. tuitensis*	-105.316833	20.354167	752	*E. Gándara et al. 3280*
19	*B. tuitensis*	-105.296389	20.35	893	*E. Gándara et al. 3282*
20	*B. elegans s. str.*	-104.390369	20.563611	1525	*J. P. Brunel et al. 891*
21	*B. elegans s. str.*	-104.394229	19.694265	1503	*E. Gándara et al. 3296*

Climate variables

For each of the 21 populations sampled, we recorded the georeferenced location (latitude, longitude, and elevation) (Table 1, Fig. 1). The bioclimate variables (Fick & Hijmans 2017) were downloaded from WorldClim (2020). Then, the coordinates for each locality and the raster files for the 19 bioclimate variables were uploaded to QGis 2.16.3 software (QGIS Development Team 2020). We extracted the 19 bioclimate variables for each locality using the plugin point sampling tool on QGis 2.16.3, for statistical analysis. We ran a Pearson's product-moment correlation, in which those with a high degree of correlation ($r > 0.7$) were excluded from the analyses. The uncorrelated climate variables were: BIO1, BIO2, BIO3, BIO4, BIO5 and BIO12.

Statistical analyses

First, based on floral variation (size, ornamentation and color) we divide *Bessera elegans s. l.* into four groups: Group 1 is composed of populations found in savanna-like vegetation at low elevations from Nayarit to Oaxaca, with a polymorphic perianth and staminal tube showing multiple colors (Moore's Group B). Group 2 is comprised of populations of *Bessera elegans s. str.* with the widest geographic distribution and that always have red or carmine perianth (Moore's Group A). Group 3 consisted of two populations from Colima, always with a purple perianth, staminal tube and filaments. Group 4 included *B. tuitensis* populations.

Second, we carried out Shapiro-Wilk's test to check the normality of the morphological variables. Then, we ran a Pearson's product-moment correlation, in which those that were highly correlated ($r > 0.7$) were excluded from the analyses. The analyses were carried out using only those parametric variables. The selected characters were: "pedicel length", "tube length", "filament length", "leaf length", and "leaf width". Then, we ran an Analysis of Variance (ANOVA) on the four groups for each normal variable. We also performed a MANOVA (Multivariate Analysis of Variance) to test if the four groups had the same multivariate mean. If the MANOVA revealed a significant overall difference between groups, we did a *post-hoc* pairwise comparison using Hotelling's *p* values. In order to evaluate morphological variation among the four *Bessera* groups, we performed a linear discriminant analysis (LDA). Finally, we applied a Mantel test, based on Pearson's product-moment correlation. This was done to test if there was a significant relationship between the variation in the five selected characters and the six uncorrelated climate variables. All statistical analyses were carried out in Past v. 4.02 (Hammer *et al*. 2001).

Conservation status

In order to evaluate the risk of extinction of the species studied, we calculated the two parameters used by the IUCN Red List of Threatened Species (IUCN 2019). We used occurrence records to evaluate the extent of occurrence (EOO) and the area of occupancy (AOO). The EOO was measured by the convex polygon and the AOO was calculated using a 2 × 2 km grid cell. EOO and AOO were estimated using GeoCat (Bachman *et al*. 2011).

Results

Summary statistics of all morphological variables are presented in Table 2. The ANOVA analysis showed statistically significant differences at $P < 0.05$ for tube length, filament length, leaf length, and leaf width, but not for pedicel length (Fig. 2A–E). The overall MANOVA analysis showed statistically significant differences among the four groups ($F = 77.69$, $P < 0.001$). Pairwise comparisons among the four groups were all statistically significantly different ($P < 0.001$).

The first two canonical axes explain 94.87% of the total variation (Fig. 2F). The confusion matrix was classified for the four groups as follows: 28 plants from group 1 were correctly classified in group 1 and two were classified in group 3. Of the 194 *Bessera elegans s. str*. plants, 163 of them were correctly classified as *Bessera elegans s. str.*, 18 were placed in group 1 and 13 in group 3. Of the 30 plants of group 3, 26 were correctly classified, and four were placed in group 1. The 30 plants of *Bessera tuitensis* were all correctly classified. The Mantel test showed a statistically significant correlation between the five morphological characters of *Bessera* populations and six climate variables ($r = 0.21$; $P = 0.04$), which means that the climate variables only explain 21% of the total morphological variation observed.

Based on the statistically significant morphological differences and the correlations between the climate variables and morphological characters found among the *Bessera* populations analyzed, below we propose and discuss the recognition of two new taxa.

Taxonomic treatment

Morphological key to *Bessera* species

1. Tepals pinkish to light lilac; perianth tube 1–2 mm long; endemic to the Sierra de El Cuale, Jalisco ..... *B. tuitensis*
- Tepals carmine, scarlet, light red, violet, purplish or fuchsia; perianth tube 7.5–17 mm long; widely distributed 2
2. Staminal tube dark purple, conical; filaments dark purple, cuneate and flattened ..... *B. ramirezii*
- Staminal tube white, whitish or violet, cylindrical; filaments scarlet, red, violet or purple, terete or semiterete 3
3. Tepals carmine, ruby or red; staminal tube white or whitish, 7.48–16.56 mm long (mean = 11.96 mm long); filaments carmine, ruby, red or violet, terete, 7.8–21.7 mm long (mean = 13.8 mm long); from the Balsas Basin, the Chihuahuan Desert, the Sierra Madre Occidental, the Sierra Madre del Sur and the Transmexican Volcanic Belt ..... *B. elegans*
- Tepals light red, scarlet, violet, magenta or fuchsia; staminal tube whitish or violet, 7.5–13.2 mm long (mean = 10 mm long); filaments violet or purple, semiterete, 5.3–10.2 mm long (mean = 7.7 mm long); the Pacific Lowlands ..... *B. elegantissima*

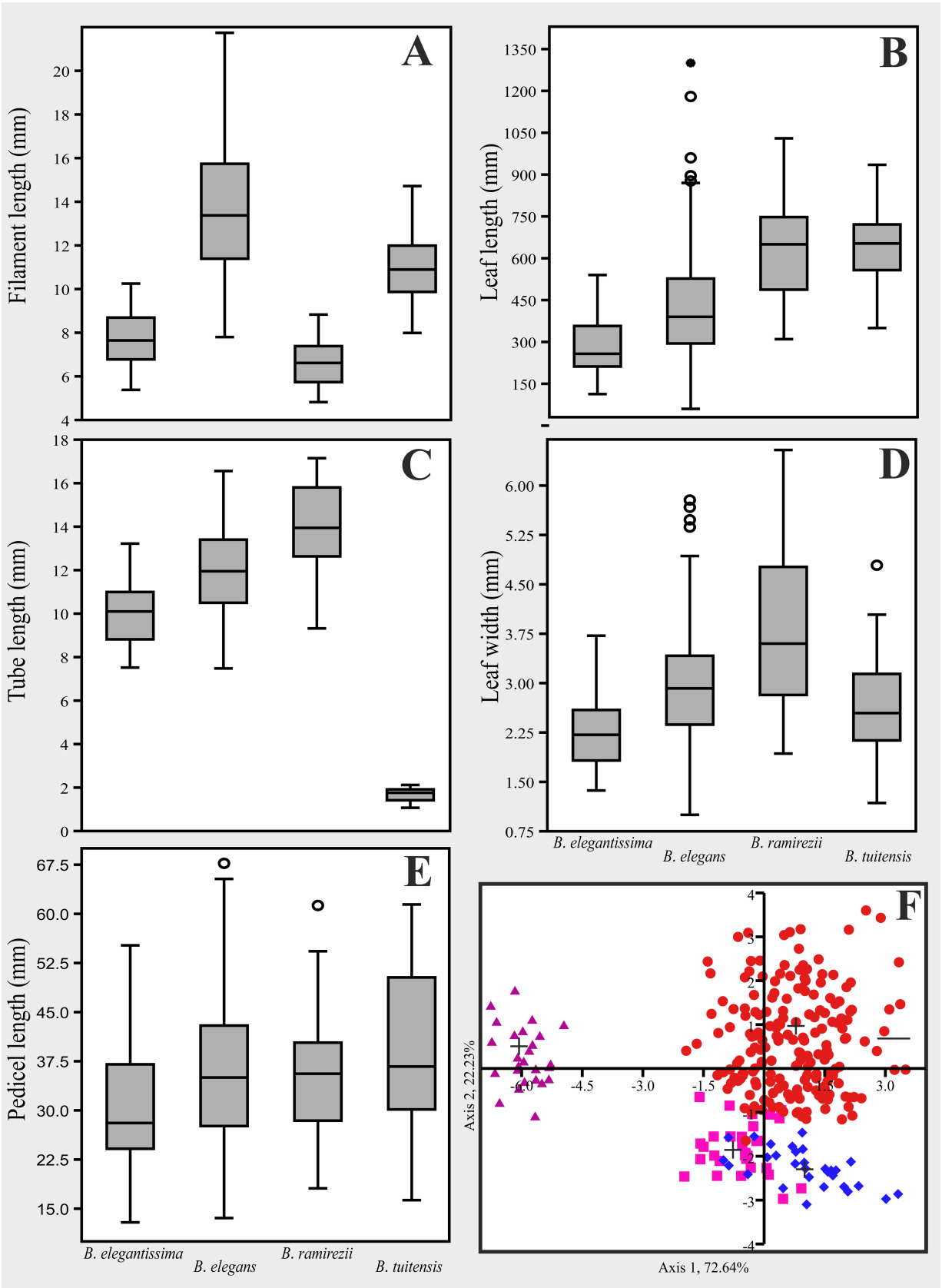

FIGURE 2. Box-plots for five characters that were significantly different among species ($P < 0.05$). A. Filament length. B. Leaf length. C. Tube length. D. Leaf width. E. Pedicel length. Boxes represent 75% of the variation and horizontal bars the other 25%; middle lines indicate the mean; whiskers indicate the range of the data; and dots indicate outliers. F. Discriminant analysis. Red circles = *Bessera elegans*, fuchsia squares = *B. elegantissima*, blue rhombuses = *B. ramirezii*, lilac triangles = *B. tuitensis*. Black crosses are the centroids for each species.

Bessera elegantissima E. Gándara, Ortiz-Brunel, Art.Castro & Ruiz-Sanchez *sp. nov.*, Figs. 3, 4 A–B

TYPE:—MEXICO. Nayarit: Acaponeta, Km 10 brecha Las Coloradas-Santa Cruz de Acaponeta, 22°31'5.5" N, 105°16'40.2" W, 80 m, 5 July 2014 (fl), *A. Castro-Castro & E. Ruiz-Sánchez 3690* (holotype: IBUG!, isotype: MEXU!).

Bessera elegantissima is similar to *B. elegans* but differs in floral size and color. *Bessera elegantissima* has a wide range of tepal colors; from light red, scarlet, and violet to magenta or fuchsia. The staminal tube is white or violet, 7.5–13.2 mm long (mean = 10 mm long), The filaments are semiterete, violet or purple, 5.3–10.2 mm long (mean = 7.7 mm long).

Perennial herbs, geophytes. **Roots** fibrous. **Corms** ovoid, 1.1–2.3 × 1–2.3 cm, with brown parallel fibers or some membranous tunics developing upward into a collar 3–23 mm long. **Leaves** 2–6(–9), 11.3–54 × 0.1–0.4 cm, linear, plano-convex or terete, glabrous, margin minutely dentate. **Inflorescences** umbellate; scape 42–84 cm × 1.4–4 mm, glabrous, sometimes pruinose; spathe bracts 2 to 6, 2–10 mm long; umbel with 4 to 13 flowers. **Flowers** on pedicels 12–55 mm long, nodding at anthesis becoming erect after; perianth 11–26 mm long; tepals 11–18.8 × 4.4–7.5 mm, lanceolate to ovate, from scarlet or light red to magenta, fuchsia or violet, with a prominent middle nerve, with two white stripes at the internal face, united at the base forming a narrow tube; stamens 6, exserted, joined to the perianth at the base; filaments violet or purple, with a portion joined into a tube by a continuous membrane forming a staminal tube 7.5–13.2 mm long, cylindrical, whitish to violet or purple, the free portion of the filaments semiterete, 5.3–10.2 mm long; anthers ellipsoid, dorsifixed, with longitudinal dehiscence, 1.2–2.4 mm long, dark green to blue or grayish blue at dehiscence; ovary ellipsoid, 1–4 mm long, style elongated, exceeding the stamens, purple-whitish, stigma 3-lobed or tubiform. **Fruits** a loculicidal capsule with apical dehiscence, oblong, 8.5–14 × 7.5–8.5 mm. **Seeds** irregular and ridged, flattened, 4–4.4 × 1.8–2 mm.

Distribution, habitat and phenology:—The populations of *Bessera elegantissima* grow from almost sea level (10 m a.s.l.) up to 1100 m a.s.l., in savanna-like vegetation *sensu* Rzedowski (1978), subdeciduous tropical forest and tropical dry forest, along the Pacific Lowlands and Balsas Basin provinces, from Sinaloa to Oaxaca. It shares habitat with the trees *Bursera* spp., *Byrsonima crassifolia* (L.) Kunth, *Brosimum alicastrum* Sw., *Chomelia* spp., *Curatella americana* L., *Erythroxylum mexicanum* Kunth, *Jacquinia* spp., *Quercus aristata* Hook. & Arn., *Q. elliptica* Née, *Q. resinosa* Liebm., *Sabal rosei* (O.F. Cook) Becc., *Tabebuia* spp., and *Trichospermum mexicanum* (DC.) Baill. Flowering specimens have been collected from June to September. Fruits have been collected from July to October.

Comparison:—*Bessera elegantissima* differs from *B. elegans* in floral size and color. *B. elegantissima* has a perianth 11.73–26.92 mm long, with tepals 11–18.8 × 4.4–7.5 mm and shows a wide range of tepal colors from light red, scarlet, violet to magenta or fuchsia; the staminal tube is 7.5–13.2 mm long, whitish to violet or purple; the filaments are 5.3–10.2 mm long, semiterete violet or purple. Meanwhile the perianth of *B. elegans* is 18.24–33.6, the tepals are 7.19–24.02 × 4.76–10.18 mm, carmine to red and the staminal tube is 7.48–16.56 mm long white or whitish, the filaments are 7.8–21.7 mm long, terete, red or violet (Table 2, Fig. 4).

Bessera elegantissima differs from *B. tuitensis* in floral size and color. The perianth of *B. tuitensis* is 13.31–21.12 mm long, the tepals are 9.92–15.88 × 3.22–6.49 mm, pinkish to lilac, the filaments are connate at the base forming a ring, 1.07–2.12 mm long, white, the filaments are 7.99–14.72 mm long, terete, white (Table 2, Fig. 4).

Bessera elegantissima differs from *B. ramirezii* in floral sizes and colors. The perianth of *B. ramirezii* is 19.63–30.87 mm long, the tepals are 13.43–18.49 × 3.93–7.71 mm, dark purple with an undulated margin, the staminal tube is 7.5–13.2 mm long, dark purple, the filaments are 4.82–8.83 mm long, flattened and cuneate, dark purple (Table 2, Fig. 4).

Etymology:—The specific epithet *elegantissima* refers to the beautiful flower colors of this species. There are up to six different flower colors in a single locality (Figs. 4 A–B).

Conservation status:—According to the EOO (255,621 km^2) and AOO (160 km^2) analysis, *Bessera elegantissima* fits the Least Concern (LC) category for the EOO analysis, and the criteria of B2a(ii) for AOO, and so should be considered Endangered (EN) (IUCN 2019).

Additional specimens examined (paratypes):—MEXICO. Guerrero: Acapulco: Parque Nacional El Veladero, Ejido Santa Cruz, 100 m, July 5, 1985, *N. Noriega-Acosta et al. 587* (MEXU!). Chilpancingo: brecha El Ocotillo-Jaleaca, aprox. 5 km, 650 m, 21 July 1991, *L.M. González-Villarreal et al. 4349* (IBUG!). Xochistlahuaca: Xochistlahuaca, 370 m, July 1984, *B. López C. 7–2* (USF). Zihuatanejo: en La Higuera, 50 km al NE de la desviación a Cd. Altamirano, 520 m, 24 July 2006, *J.C. Soto-Núñez 9676* (MEXU!). Jalisco: Casimiro Castillo: 3 miles north of La Resolana, 450 m, 6 July 1949, *R.L. 1543* (MEXU!). Cuautitlán de García Barragán: 6.5–7.5 km al NE de Cuautitlán 2 km al SE de Cuzalapa, 800 m, 26 July 1989, *L. Robles et al. 806* (MEXU!). Cihuatlán: al S de Cihuatlán, ladera N de Rancho El Cihualteco, 13 m, 18 July 1985, S. *Govea-Ayvar s.n.* (IBUG!). Puerto Vallarta: Fraccionamiento Sendero de Luna,

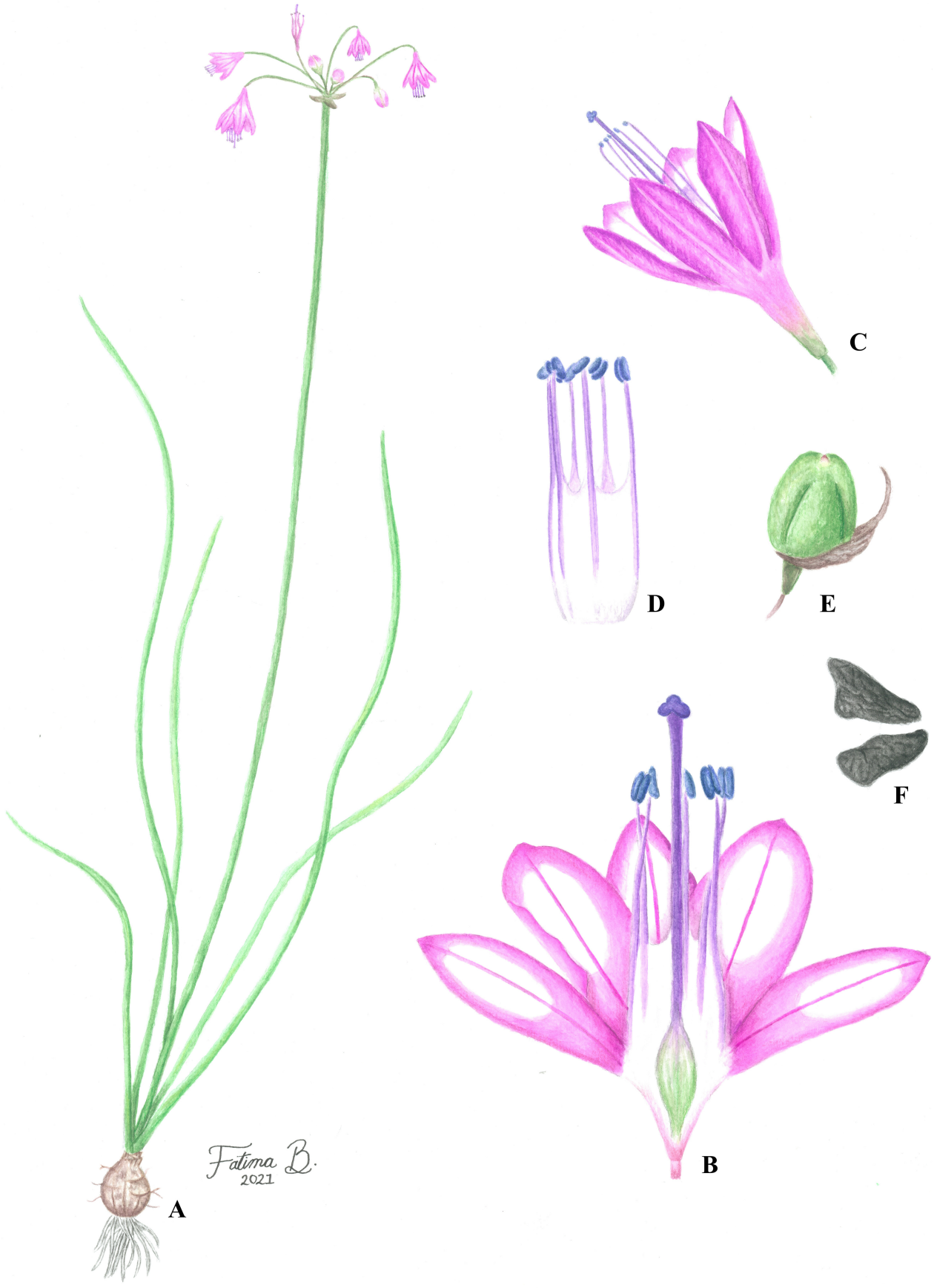

FIGURE 3. *Bessera elegantissima*. A. Complete plant with corms, leaves, inflorescence and flowers. B. Dissected flower. C. Flower, lateral view. D. Membranous staminal tube with filaments and anthers. E. Fruit. F. Seeds. Watercolor illustration by Fátima Bracamontes.

terreno localizado el E del estero El Salado, justo a un lado de la Universidad del Valle de México y el basurero municipal, 40 m, 2 August 2008, *A. Castro-Castro et al. 1325* (IBUG!). Michoacán: Múgica: camino de Nueva Italia a la presa Francisco J. Múgica, 429 m, 8 August 2011, *J. Cortés-Flores 185* (IBUG!, MEXU!). Tiquicheo de Nicolás Romero: en La Crucita, 18 km al SO de Tiquicheo, 600 m, 11 July 1982, *J.C. Soto-Núñez 4070* (MEXU!). Nayarit: Acaponeta: route 15, ca. 88 km southeast of Escuinapa, 60 m, 12 July 1966, *R. Cruden 1048* (MEXU!); a 3.3 km al SW de la Mesa de Pedro y Pablo, 780 m, 12 September 1989, *O. Téllez 12019* (MEXU!); km 10 brecha Las Coloradas-Santa Cruz de Acaponeta, 80 m, 5 July 2014, *A. Castro-Castro & E. Ruiz-Sánchez 3690* (IBUG!, MEXU!). Bahía de Banderas: Punta Mita, 22 July 1932, *J.T. Howell 10377* (GH!, US!). Rosamorada: km 96 carretera libre Tepic-Acaponeta, cerca del ejido La Providencia, 58 m, 1 August 2009, *A. Rodríguez & A. Castro-Castro 5792* (IBUG!); carretera 15, Tepic-Mazatlán km 56, 14 km después de la desviación a Las Peñas, 18 m, 22 July 2020, *E. Ruiz-Sanchez & E. Gándara 655, 656, 657, 658* (IBUG). Ruíz: San Pedro Ixcatán, 5 km al N de San P. Ixcatán rumbo al Río San Pedro, alrededores del Puerto Los Tepetates y la cañada Los Bueyes, cerca de El Pozolillo, 150 m, 19 July 2007, *A. Castro-Castro et al. 945* (IBUG!); Paso de los Bueyes, 230 m, 2 July 2009, *R. Ramírez-Delgadillo et al. 7675* (IBUG!). San Blas: km 4 de la carr. a San Blas, del entronque con carr. Tepic-Mazatlán, 95 m, 6 August 1987, *O. Téllez et al. 10718* (MEXU!); alrededores de la planta de asfalto, 160 m, 6 July 1991, *A. Benítez-Paredes 3227* (MEXU!). Santa María del Oro: área de ordenamiento y banco de material El Paraíso, 350 m, 28 June 2000, *E. Rosales et al. 4353* (MEXU!). Santiago Ixcuintla: carretera 15 Tepic-Mazatlán a 1 km después de El Capomal, 73 m, 21 July 2020, *E. Ruiz-Sanchez & E. Gándara 654* (IBUG). Tepic: ca. 1 mi SW of intersection of San Blas road and Tepic-Mazatlán road, 210 m, 25 June 1972, *G.L. Webster & S. Lynch 17079* (MEXU!); km 20 carr. Tepic-Mazatlán, 652 m, 6 July 2004, *A. Rodríguez & C. Briseño 3662* (IBUG!); km 34–35 carretera de cuota Tepic-Mazatlán, 68 m, 1 August 2009, *A. Rodríguez & A. Castro-Castro 5785* (IBUG!). Oaxaca: San Carlos Yautepec: San Miguel Chongo, 500 m al N sobre la vereda a San Pedro Sosoltepec, 410 m, 30 August 2000, *N. Velázquez R. 308* (MEXU!); San Miguel Chongo, 1.5 km al W, 450 m, 28 September 2000, *N. Velázquez R. 434* (MEXU!). San Juan Colorado: camino del cerro de La Ardilla, cerro de la lluvia (Yucu Savi) 524 m, 15 July 2013, *M.I. Mejía-Marín 243* (MEXU!). San Miguel del Puerto: Santa María Xadani, 2 km al N, 430 m, 24 June 2000, *S.H. Salas-M. 3000* (MEXU!); 2.7 km aprox. al noroeste del Rancho San Agustín sobre el camino a la Finca La Colorada, 770 m, 23 August 2001, *A. Saynes et al. 2593* (MEXU!); 1.5 km de la carretera para el cerro de Santa María Xadani, 800 m, 6 October 2001, *J. Pascual 43* (MEXU!). Santiago Pinotepa Nacional: ca. 24 km E of the Oaxaca-Guerrero state line W of Pinotepa Nacional, 160 m, 22 July 1991, *Mayfield et al. 988* (MEXU!). Villa de Tutepec de Melchor Ocampo: 11 km al N de Río Grande, brecha a San Marcos Zacatepec, 100 m, 6 July 1992, *Á. Campos 4658* (MEXU!). Sinaloa: Concordia: 3.2 km después de La Guasimita rumbo a Pánuco, 27 July 2003, *J. Ceja et al. 1449* (MEXU!); El Pirame, near Cerro El Cinco, ca. 8 km (by air) north of El Magistral, Comunidad La Guasima, 827 m, 19 September 2005, *T.R. Van-Devender 1443* (CIAD!); comunidad La Guásima, 290 m, 4 July 2008, *M. Ruíz-Guerrero et al. 15* (CIAD!); comunidad La Guásima, 782 m, 22 September 2009, *M. Ruíz-Guerrero et al. 195* (CIAD!); comunidad La Guásima, 272 m, 3 August 2010, *M. Ruíz-Guerrero et al. 370* (CIAD!); comunidad La Guásima, 754 m, 28 September 2010, *M. Ruíz-Guerrero et al. 446* (CIAD!). Mazatlán: loam flat, n. of Mazatlan, 20 m, 16 August 1935, *F.W. Pennell 19738* (MEXU!). Rosario: between Rosario and Colonias, 12 July 1897, *J.N. Rose 1611* (MEXU!); a 16.5 km al NE de Chililos, 145 m, 26 July 1983, *E. Martínez et al. 4027* (MEXU!). San Ignacio: 2 mi west of San Ignacio, on road to San Ignacio from highway 15, 15 July 1962, *E. Molseed 4* (MEXU!).

Bessera ramirezii E. Gándara, Ortiz-Brunel, Art.Castro & Ruiz-Sanchez *sp. nov.*, Figs. 4 C–D, 5 A–F

TYPE:—MEXICO. Colima: Colima, 19 km al suroeste de Colima, camino a Tecomán, 19°4’7.8” N, 103°46’41.9” W, 570 m, 4 August 2011 (fl), *A. Rodríguez et al. 6317* (holotype: IBUG!, isotype: MEXU!).

Bessera ramirezii is similar in form to *B. elegans* and *B. elegantissima* but differs in having the perianth dark purple; staminal tube purple, conical and flattened with cuneate filaments.

Perennial herbs from a corm. **Roots** fibrous. **Corm** ovoid, 1.6–3.2 × 1.7–4 cm, with brown parallel fibers and membranous tunics, collar 7–16(–27) mm long. **Leaves** 2–5(–8), 31–103 × 0.2–0.6 cm, linear, plano-convex, glabrous, margin minutely dentate. **Inflorescence** umbellate; scape 38–100 cm × 2–3.5 mm, glabrous at its upper portion and scabrous to dentate lower down; spathe bracts 2–4(–7), 6–11 mm long; umbel with 4 to 29 flowers. **Flowers** on pedicels 18–61 mm long, nodding at anthesis becoming erect after; perianth 19–31 mm long; tepals 13–19 × 3.9–7.8 mm, lanceolate to ovate, purple, with a prominent middle nerve, white striped at the internal face, united at the base forming a narrow tube, with an undulated margin; staminal tube 9–17 mm long, conical, stamens 6, exserted, joined to the perianth at the base; filaments dark purple, partially joined into a staminal tube by a continuous membrane;

the free portion of the filaments cuneate, flattened, 4.8–8.8 mm long; anthers ellipsoid, dorsifixed, with longitudinal dehiscence, 0.7–1.2 mm long, blue; ovary ellipsoid, 1–4 mm long, style elongated, exceeding the stamens, purple, stigma 3-lobed or tubiform. **Fruit** a loculicidal capsule with apical dehiscence, oblong, 12.8–15.7 × 7.5–8.5 mm. **Seeds** irregular and slightly ridged, flattened, 3.5–4.2 × 1.8–2.2 mm.

Distribution, habitat and phenology:—The populations of *Bessera ramirezii* grow from 430 to 1700 m a.s.l., in tropical dry forest mainly or at the ecotone between oak forest and tropical dry forest. Where they grow, the soils are calcareous in origin. Also, one population is located on gypsum outcroppings. This species is only known from a few populations in the states of Colima and Jalisco in the Sierra Madre del Sur and the Pacific Lowlands provinces (Fig. 1). It shares habitat with the trees *Bursera* spp., *Ceiba aesculifolia* (Kunth) Britten & Baker f., *Cnidosculus* sp., *Eysenhardtia polystachya* (Ortega) Sarg., *Lysiloma* spp., *Manihot* sp., *Plumeria rubra* L., *Quercus* spp., *Thouinia acuminata* S. Watson and *Ziziphus mexicana* Rose. Flowering specimens have been collected from June to October. Fruits have been collected from July to November.

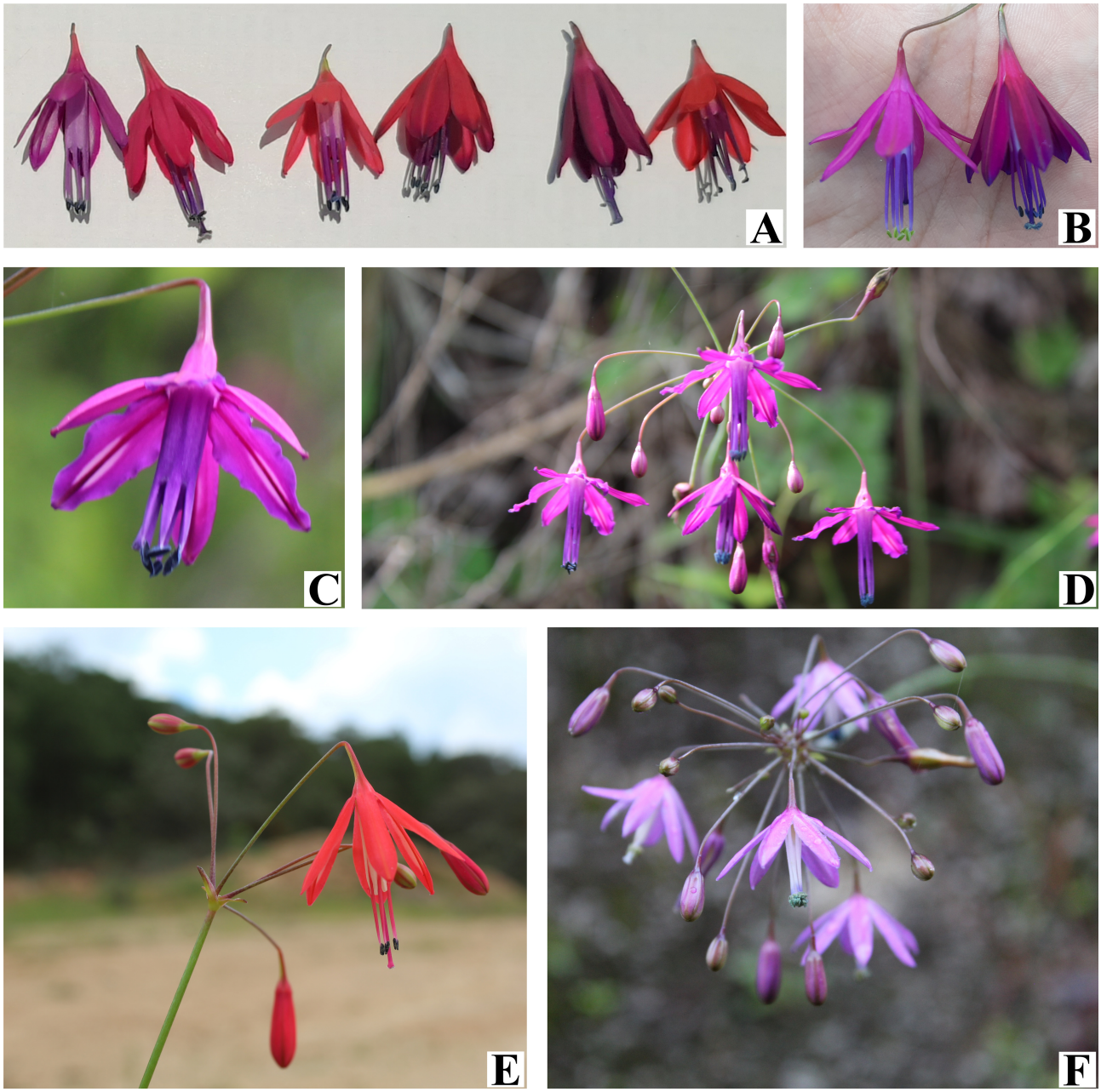

FIGURE 4. A. *Bessera elegantissima*, different perianth colors found in a single locality. *B. elegantissima* showing two different perianth and anther colors. C. Close-up of *Bessera ramirezii,* showing membranous staminal tube, flat filaments and anthers. D. *B. ramirezii* inflorescence showing some open flowers. E. Typical scarlet perianth of *Bessera elegans*. F. *Bessera tuitensis* inflorescence and flowers. Photos by Juan Pablo Ortiz-Brunel (C–F) and Eduardo Ruiz-Sanchez (A, B).

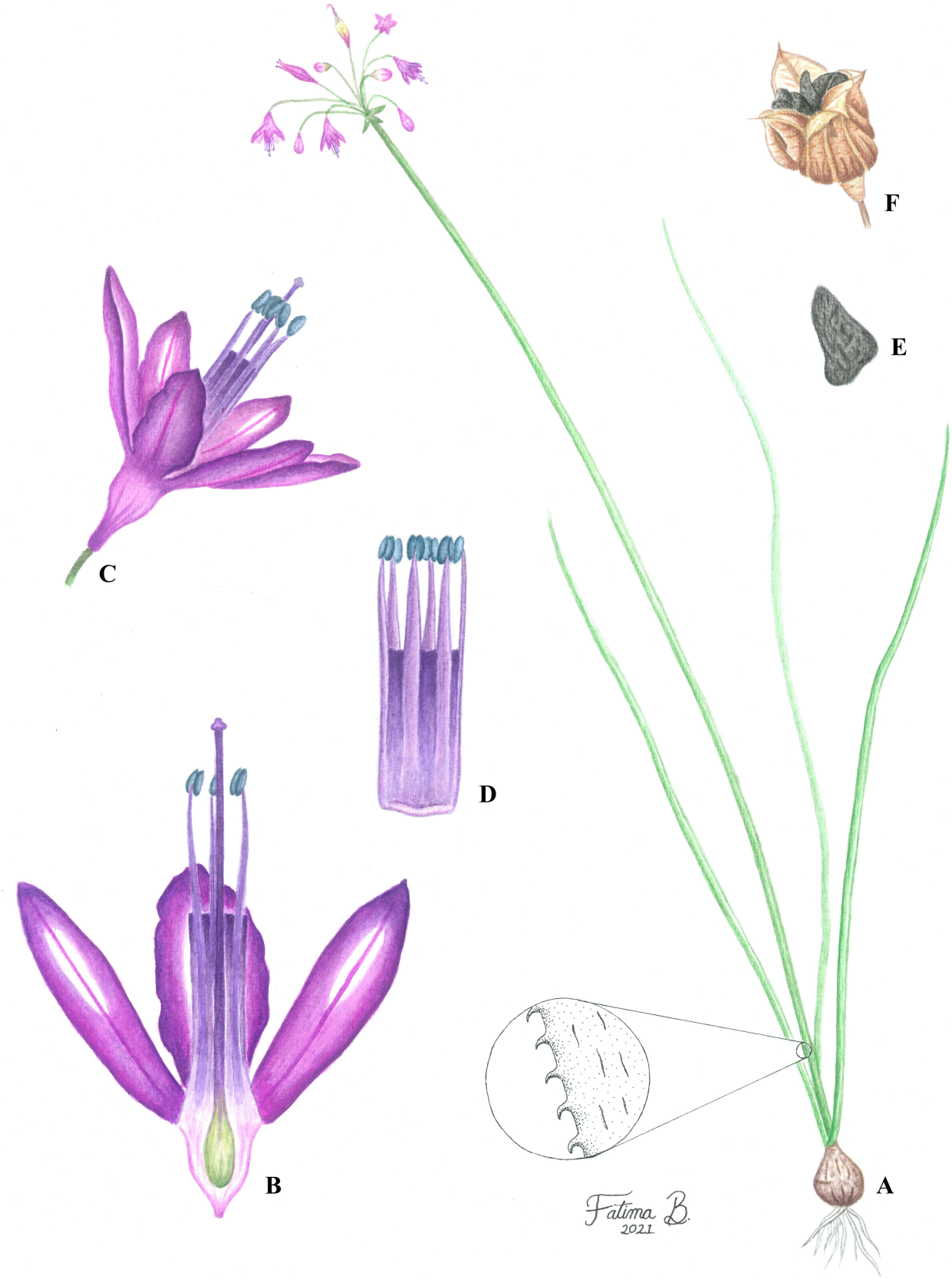

FIGURE 5. *Bessera ramirezii*. A. Complete plant with corms, leaves, inflorescence, flowers, and detail of scabrous scape at the base. B. Dissected flower. C. Flower, lateral view. D. Membranous staminal tube with filaments and anthers. E. Fruit. F. Seed. Watercolor illustration by Fátima Bracamontes.

TABLE 2. Morphological characters measured for the *Bessera* species/populations/plants in western Mexico.

	Scape length (mm)	Pedicel length (mm)	Perianth length (mm)	Tepal length (mm)	Tepal width (mm)	Staminal tube and filament length (mm)	Staminal tube length (mm)	Filament length (mm)	Leaf length (mm)	Leaf width (mm)
Bessera elegans										
N	194	194	194	194	194	194	194	194	194	194
Min	305	13.57	18.24	7.19	4.76	19.028	7.48	7.8	60	1
Max	970	67.71	33.6	24.02	10.18	36.16	16.56	21.74	1300	5.78
Mean	583.28	36	25.92	18.54	7.05	25.79	11.96	13.82	424.86	2.94
S. E	9.48	0.77	0.212	0.16	0.06	0.24	0.14	0.2	13.59	0.06
S. D.	132.04	10.81	3.04	2.26	0.95	3.34	2	2.85	189.36	0.85
Bessera tuitensis										
N	26	26	26	26	26	26	26	26	26	26
Min	420	16.3	13.31	9.92	3.22	9.1	1.07	7.99	350	1.18
Max	890	61.43	21.12	15.88	6.49	16.14	2.12	14.72	935	4.79
Mean	624	38.6	17.5	13.14	5.1	12.67	1.68	11.0	636.84	2.65
S. E.	25.24	2.41	0.43	0.43	0.25	0.17	0.06	0.31	26.66	0.14
S. D.	128.73	12.31	2.21	2.21	1.27	0.89	0.32	1.6	135.47	0.75
Bessera elegantissima										
N	30	30	30	30	30	30	30	30	30	30
Min	422	12.91	11.73	11.95	4.42	14.17	7.52	5.38	113.1	1.37
Max	840	55.19	26.92	18.81	7.68	23.43	13.22	10.25	540	3.72
Mean	649.1	31.3	21.63	14.81	6.17	17.77	10.0	7.74	287.47	2.31
S. E.	17.5	1.97	0.57	0.3	0.13	0.38	0.26	0.26	20.97	0.11
S. D.	95.9	10.79	3.12	1.65	0.75	2.08	1.45	1.43	114.85	0.61
Bessera ramirezii										
N	30	30	30	30	30	30	30	30	30	30
Min	380	18.1	19.63	13.43	3.93	15.99	9.32	4.82	310	1.93
Max	990	61.28	30.87	18.49	7.71	23.26	17.15	8.83	1030	6.54
Mean	651	35.9	26.3	16.21	5.98	20.58	13.9	6.67	622.7	3.83
S. E.	28.1	1.75	0.5	0.27	0.14	0.32	0.38	0.17	33.25	0.21
S. D.	153.94	9.58	2.78	1.49	0.78	1.78	2.08	0.95	182.14	1.19

N. Number of plants measured; S. E. Standard Error; S. D. Standard Deviation

Comparison:—*Bessera ramirezii* differs from *B. elegans* in floral size and color. All the plants from the two populations of *B. ramirezii* have flowers bigger than *B. elegans* and have perianth, tepals, staminal tube and filaments dark purple. Perianth in *B. ramirezii* is 19.63–30.87, tepals are 13.43–18.49 × 3.93–7.71 mm, and have an undulated margin, staminal tube is 9.32–17.15 mm long, filaments are 4.82–8.83 mm long and flat–cuneate. The perianth of *B. elegans* is 18.24–33.6 mm long, tepals are 7.19–24.02 × 4.76–10.18 mm long, carmine to red and the staminal tube is 7.48–16.56 mm long white or whitish, filaments are 7.8–21.7 mm long, terete, red or violet (Table 2; Fig. 4).

Bessera ramirezii can be easily distinguished from *B. elegantissima*: it is smaller, with a perianth 11.73–26.92 mm long, tepals 11–18.8 × 4.4–7.5 mm and has a wide range of tepal colors from light red, scarlet, violet to magenta or fuchsia; the staminal tube is 7.5–13.2 mm long, whitish to violet or purple; the filaments are 5.3–10.2 mm long, semiterete violet or purple (Table 2; Fig. 4).

Finally, *Bessera ramirezii* is quite different from *B. tuitensis*, because the perianth of *B. ramirezii* is 13.31–21.12, the tepals are 9.92–15.88 × 3.22–6.49 mm, pinkish to lilac, the filaments are connate at the base forming a ring, 1.07–2.12 mm long, white, the filaments are 7.99–14.72 mm long, terete, and white (Table 2, Fig. 4).

Etymology:—The specific epithet honors the memory of Raymundo Ramírez Delgadillo (1968–2011), professor of the Universidad de Guadalajara, Mexico. He described *Bessera tuitensis* and told us about the possibility that this plant was a different species when we showed him the results of the phylogenetic analysis by Gándara *et al.* (2009). We have lovingly remembered Raymundo Ramírez Delgadillo over the ten years since he passed away.

Conservation status:—According to the results of the EOO (475.3 km^2) and AOO (40 km^2) analysis, this species fits criteria B1ab(i)+2ab(ii) and should be considered Endangered (EN) (IUCN 2019).

Additional specimens examined:—MEXICO. Colima: Colima: mountains summit near pass ca. 11 miles south-southwest of Colima on Manzanillo road, 500 m, 18 July 1957, *R. McVaugh 15552* (MEXU!); route 110 between km 17 and 18 ca. 17.5 km S of Colima, 500 m, 18 June 1971, *R. Cruden 1885* (MEXU!); 8 km delante de la desviación a Los Asmoles, carretera Colima-Manzanillo, 490 m, 29 July 1989, *A.R. López-Ferrari et al. 917* (MEXU!); 19 km al Suroeste de Colima, camino a Tecomán, 570 m, 4 August 2011, *A. Rodríguez et al. 6317* (IBUG!, MEXU!); camino de ascenso al cerro La Cumbre, a 100 km de la intersección con la carretera Méx. 110 entre Colima y Pihuamo, 450 m, 11 August 2005, *A. Rodríguez & A. Castro-Castro 4331* (IBUG!, MEXU!); 20.5 km al SW de Colima por la carretera Colima-Manzanillo, 431 m, 11 August 2005, *A. Rodríguez & A. Castro-Castro 4332* (IBUG!, MEXU!). Comala: Sitio 39, 3.3 km en línea recta al N de Campo Cuatro, camino a Lagunitas, 21 August 2002, *G. Ibarra-Manríquez 5766* (MEXU!); 12.5 km a partir de Juluapan, camino a Campo Cuatro, 1220 m, 11 October 2018, *J.P. Ortiz-Brunel et al. 549* (IBUG!); camino Juluapan a Campo Cuatro, 1049 m, 24 July 2020, *E. Gándara et al. 3258* (IBUG!); camino Juluapan-Campo Cuatro, 1049 m, 25 July 2020, *J.P. Ortiz-Brunel et al. 828* (IBUG!). Minatitlán: 8–9 km al NEE de Minatitlán, 5–7 km al SEE de El Sauz, 1550 m, 3 October 1988, *R. Cuevas & G. López 3301* (IBUG!, MEXU!); Cerro Grande, brecha que va de El Sauz a El Terrero, 1550 m, 1 August 1989, *M. Cházaro B. 6026* (IBUG!); 8 km de El Sauz camino al Terrero-9–10 km al NE de Minatitlán, 1700 m, 24 August 1989, *F.J. Santana-Michel 4509* (MEXU!); 9–10 km al ENE de Minatitlán, km 7 y 8 de El Saúz al Terrero, Camino El Saúz-El Terrero, 1600 m, 26 July 1991, *F.J. Santana-Michel et al. 5214* (IBUG!, MEXU!); camino a El Terrero, 1651 m, 25 July 2020, *E. Gándara et al.* 3262 (IBUG!). Jalisco: Tolimán, brecha a Campo Cuatro, Sierra de Manantlán, 1500 m, 2 August 1990, *R. Ramírez-Delgadillo 2170* (IBUG!).

Discussion

Moore (1953) published a morphological review of *Bessera elegans* and identified three morphological groups, which he called groups A, B, and C. Group A corresponds to *B. elegans s. str*. and has the widest geographic distribution. Meanwhile, Group B corresponds to those plants growing along the Pacific Lowlands and the Balsas Basin provinces. Finally, Moore's Group C corresponds to a single locality from Punta de Mita, Nayarit, close to Puerto Vallarta, Jalisco. The morphological differences found by Moore (1953) among these three groups were the number of flowers per umbel, pedicel length, perianth length and color. In this study, we included two populations of *B. tuitensis* and two populations of *B. ramirezii* (not included in Moore's revision). We found statistically significant differences at $P < 0.05$ for tube length, filament length, leaf length and leaf width, but not for pedicel length among our four groups (i.e. species). Contrary to Moore's (1953) observation, pedicel length did not differ among groups (Table 2, Fig. 2E). Additionally, we found that filament length, leaf length, and leaf width differed among groups (Fig. 2 A–B, D).

We divided our sampling into four species groups: *Bessera elegans s. str*., *B. tuitensis* and the newly described species *B. elegantissima* and *B. ramirezii*. Our results (MANOVA) showed statistically significant differences among the four groups and pairwise comparisons among the four groups were all statistically significantly different. The LDA analysis showed that most of the variation is explained by the two canonical axes (94.87%). The confusion matrix correctly classified all *B. elegantissima* and *B. tuitensis* plants as their respective species. For *B. ramirezii* 26 of the 30 plants were correctly classified as this species, and the other four into *B. elegantissima*. However, both species can be easily recognized by a combination of their morphological characters. Here, we recognize Moore's (1953) Group B as a distinct species, which we have named *B. elegantissima* and that differs in size and color from *B. elegans s. str.* Besides groups A and B, Moore (1953) recognized third group: Group C, with 3–5 flowers per umbel, blue-violet or violet, pedicels 6–8 cm long. The perianth is 6 mm long and the tepals are 13–15 mm long. Moore (1953) included a single specimen for this group (*Howell 10377*; GH, US). We examined this specimen, which is deposited at the US herbarium. (https://ids.si.edu/ids/media_view?id=ark:/65665/m3b2aec5ff04714cfa9f37a8d706beafab&defaultView=image_dynamic accessed on March 17, 2021). Additionally, we examined another specimen deposited at the IBUG herbarium (*A. Castro-Castro et al. 1325*) that was collected in Puerto Vallarta, Jalisco, fairly close to the collection made by John Thomas Howell in 1932. Based on the results of our study, we think both specimens belong to *B. elegantissima*.

According to *Bessera*'s geographic distribution (Fig. 1), none of its species are sympatric. During fieldwork collections, we did not find any of the four *Bessera* species growing together. The populations of *B. elegantissima* are distributed from Sinaloa to Oaxaca along the Pacific Lowlands and the Balsas Basin provinces (Fig. 1). This species grows from 10 m to 1100 m a.s.l., in savanna-like vegetation, subdeciduous tropical forest and tropical dry forest. Meanwhile, the populations of *B. ramirezii* are endemic to a small area in the states of Colima and Jalisco (Fig. 1). This species grows from 430 to 1700 m a.s.l., in tropical dry forest mainly or at the ecotone between oak forest and tropical dry forest (Rzedowski 1978). The substrate where these populations grow are soils of calcareous origin. According to our AAO results analysis, both species should be considered Endangered (IUCN 2019).

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