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A new cryptic species in *Behria* (Asparagaceae, Brodiaeoideae), from the Baja California peninsula, Mexico

EVELVINA GÁNDARA^{1,5}, JUAN PABLO ORTIZ-BRUNEL^{2,3,6}, MARKO GÓMEZ-HERNÁNDEZ^{4,7} & EDUARDO RUIZ-SANCHEZ^{2,3,8,*}

¹Facultad de Ciencias Biológicas, Benemérita Universidad Autónoma de Puebla, Ciudad Universitaria, Av. San Claudio s/n, Puebla, Puebla, 72570, Mexico

²Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Camino Ing. Ramón Padilla Sánchez 2100, Nextipac, Zapopan, Jalisco, 45200, Mexico

³Laboratorio Nacional de Identificación y Caracterización Vegetal (LaniVeg), Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Camino Ing. Ramón Padilla Sánchez 2100, Nextipac, Zapopan, Jalisco, 45200, Mexico

⁴CONACYT – Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca, Mexico

⁵etelvina.gandara@gmail.com; <https://orcid.org/0000-0001-6866-6923>

⁶juanpbrunel@gmail.com; <https://orcid.org/0000-0002-0695-8143>

⁷mrk.gmz@gmail.com; <https://orcid.org/0000-0002-6913-7027>

⁸ruizsanchez.eduardo@gmail.com; <https://orcid.org/0000-0002-7981-4490>

*Author for correspondence: ruizsanchez.eduardo@gmail.com

Abstract

Behria is a genus of petaloid geophytes endemic to the Cape Region of Baja California Sur, Mexico. It belongs to the Milla clade within the subfamily Brodiaeoideae of the Asparagaceae family. Currently, *Behria tenuiflora* is the only recognized species within this genus. In our methodological approach, we considered two distinct floral morphotypes: Group A consists of populations found at lowland elevations (10–150 m), while Group B comprises plants growing at mid to high elevations (400–2060 m). The aim of our study was to investigate whether there are discernible morphological differences and correlations with climate variables between *Behria* Group A and Group B. To address this, we measured nine quantitative characters for 94 plants from seven populations of *Behria tenuiflora*. Our findings revealed statistically significant differences ($P < 0.05$) in pedicel length, perianth length, perianth base diameter, and perianth aperture diameter of the analyzed *Behria* groups. Based on these results, we propose the recognition of *Behria leonis* as a new species. Additionally, we provide a morphological key for distinguishing *Behria* and *Bessera* genera, along with illustrations, a distribution map, and photographs.

Key words: *Bessera*, geophytes, morphological data, climatic preferences, Sierra de la Laguna

Resumen

Behria es un género de plantas geófitas petaloides endémico de la Región del Cabo de Baja California Sur, México. Perteneció al clado Milla dentro de la subfamilia Brodiaeoideae de la familia Asparagaceae. Actualmente, *Behria tenuiflora* es la única especie reconocida dentro de este género. En nuestro enfoque metodológico, consideramos dos morfotipos florales distintos. El Grupo A está formado por poblaciones encontradas en elevaciones bajas (10–150 msnm), mientras que el Grupo B comprende plantas que crecen en elevaciones medias a altas (400–2060 msnm). El objetivo de nuestro estudio fue investigar si existen diferencias morfológicas discernibles y correlaciones con variables climáticas entre *Behria* Grupo A y Grupo B. Para abordar esto, medimos nueve caracteres cuantitativos de 94 plantas de siete poblaciones de *Behria tenuiflora*. Nuestros hallazgos revelaron diferencias estadísticamente significativas ($P < 0.05$) en la longitud del pedicelo, la longitud del perianto, el diámetro de la base del perianto y el diámetro de la abertura del perianto de los grupos A y B de *Behria* analizados. Basándonos en estos resultados, proponemos el reconocimiento de *Behria leonis* como una nueva especie. Además, aportamos una clave de identificación morfológica para distinguir los géneros *Behria* y *Bessera*, y elaboramos ilustraciones, un mapa de distribución geográfica y añadimos fotografías.

Palabras-clave: *Bessera*, datos morfológicos, geófitas, preferencias climáticas, Sierra de la Laguna

Introduction

Behria Greene (1886: 143) represents a monotypic genus of petaloid geophytes with controversial systematics. It is endemic to the Cape Region of southern Baja California Sur, Mexico, including the southern Gulf of California Islands (San José, Espíritu Santo and Cerralvo). *Behria* and seven other genera are recognized in the Milla clade of the subfamily Brodiaeoideae Traub (1972: 131), in the Asparagaceae family (Pires *et al.* 2001, Pires & Sytsma 2002, Chase *et al.* 2009, Gándara *et al.* 2009, 2014, Gutiérrez *et al.* 2017). Based on molecular and morphological data, Gándara *et al.* (2009, 2014), Córdova Maqueda (2019), and Gutiérrez *et al.* (2010) confirmed *Behria* and *Bessera* Schultes f. (1829: 121) as two different genera. Later, Gutiérrez *et al.* (2017) considered *Behria* and *Bessera* as a single genus. Additionally, Gutiérrez *et al.* (2017) stated that *Bessera*, including *B. tenuiflora* (Greene) Macbride (1918: 11), has a T-shaped leaf vascular bundle, which they considered a synapomorphy. However, they did not include the length of the staminal tube formed by the connation of filaments in *Bessera*, which is absent in *Behria*, and coded the T-shaped leaf bundle as a missing data in *B. tenuiflora* (see Appendix 2, character 36. Filaments connation: absent = 0, present = 1; character 10, vascular bundle shape: “t” shape = 0, arc or “v” shape = 1). Also, Gutiérrez *et al.* (2010) mentioned that both genera form a “tube as result of filaments’ connation” and they referred it into figure 3G in their work; but such figure 3G corresponds to *Bessera elegans* Schultes f. (1829: 121) and they did not include any image of *Behria tenuifolia* Greene (1886: 143) that would confirm their assertion.

Different phylogenetic hypotheses have shown that *Behria* and *Bessera* are two different genera (Gándara *et al.* 2009, 2014, Córdova Maqueda 2019). Gándara *et al.* (2009) included four individuals of *Behria tenuiflora*, nine of *Bessera elegans*, and one of *Bessera tuitensis* Ramírez-Delgadillo (1992: 131). They used the chloroplast spacer *psbK-psbI* and morphological characters. The strict consensus tree based on combined data supports the recognition of both genera (Gándara *et al.* 2009). Later, Gándara *et al.* (2014) included two *Behria tenuiflora*, five *Bessera elegans*, and two *Bessera tuitensis* individuals. They used the chloroplast intron *rpl16* and the *psbK-psbI* spacer, and two nuclear genes (*ETS* and *ITS*). The 50% majority rule consensus tree based on concatenated data retrieved *Behria* and *Bessera* as separated genera (Gándara *et al.* 2014). Gutiérrez *et al.* (2017) used the chloroplast spacers *trnL-trnF*, *psbK-psbI*, the nuclear *ITS*, and morphological characters. The sampling included one *Bessera tenuiflora*, five *Bessera elegans* individuals, and one *Bessera tuitensis*. The 50% majority rule consensus tree based on concatenated data retrieved *Bessera tenuiflora* as the first divergent lineage and the rest of *Bessera* as a clade, but the authors did not recognize the separation of both genera. Finally, Córdova Maqueda (2019) also concluded that *Behria* and *Bessera* are separated genera, based on a morphometric and genetic study which included 32 vegetative and floral characters from 262 individuals and a distance tree based on AFLPs. The sampling considered one population of *Behria* and 18 populations of *Bessera*.

Based on previous molecular and morphological phylogenetic analyses, we recognize *Behria* and *Bessera* as two different genera. The morphological characters that differentiate them include perianth shape (tubular in *Behria* and campanulate in *Bessera*) and the arrangement of tepals (fused tepals or gamotepalous in *Behria* and free tepals or polytepalous in *Bessera*). Also, the staminal tube is absent in *Behria* and it is present in *Bessera*. Geographical distribution is another factor that distinguishes them. *Behria* is exclusively found in southern Baja California Peninsula separated from the remaining continental species of *Bessera* by an effective geographical barrier as represented by the Sea of Cortés, which originated between Late Miocene and Early Pliocene (~8.6 Ma) (Gándara *et al.* 2009, 2014, 2021).

Behria tenuiflora is currently the sole recognized species of the genus. It is restricted to southern Baja California Sur and can be found from the sea level up to 2000 meters of elevation in locations such as Pichilingue Bay, San José del Cabo, Todo Santos, and Sierra de la Laguna (León de la Luz & Pérez Navarro 2004). As the holotype was never found, León de la Luz & Navarro Pérez (2004) designated a neotype for this species: Neotype: HCIB 15992; Isonotypes: MEXU, SD, UAMIZ. Mexico, Baja California Sur, Mpio. Los Cabos, San José del Cabo, 5 km east of San Bernabé along the road towards Palo Escopeta, 23°08' N, 109°39' W, elevation of 130 m, 11 November 2000, Hilly terrain with regosol soil, characterized by a sandy-loamy texture derived from alluvial deposits originating from granitic rocks, José Luis León de la Luz 9857. Moore (1953) initially classified *Behria tenuiflora* as *Bessera tenuiflora*, and identified two distinct floral morphotypes referred to as Group A and Group B. The Group A represents the type material and displays a small perianth 18–22(–25) mm long. It is widest at the junction of the tube and ovary, often exhibiting prominent sac-like structures, and tapers into a slender throat with short, narrow lobes 2–4 mm long and 1–2 mm wide. The margins of these lobes are deep purple colored. In contrast, Group B presents a larger perianth of 22–25(–30) mm in length. It is narrower and generally less prominently sac-like at the base, gradually widening

towards the throat, and possesses longer and wider lobes (3–)4–7 mm long and 3–5 mm wide. The lobes of Group B lack dark marginal coloring. Geographically, Group A plants are predominantly found in low-elevation areas, while Group B plants occur in mid to high-elevation regions.

Romero-Schmidt *et al.* (1995) conducted a morphometric analysis of three different populations of *Behria tenuiflora*, including two populations belonging to Moore’s Group A and one of Group B. Their findings indicated the presence of at least three ecotypes of *B. tenuiflora* in the Cape Region. Building upon this information, our objective was to examine whether there are observable morphological differences, as well as correlations with climate variables between *Behria* Moore’s Group A and Group B. Additionally, we aimed to determine if Moore’s Group B corresponds to a new species to preserve both lineages.

Materials and methods

Study site:—The study site was located at the southernmost region of the Baja California Peninsula, known as Cape Region (Fig. 1). According to León de la Luz & Coaria Benet (1993) and León de la Luz *et al.* (2000), three different plant communities are found in the region. The sarcocaulous scrubland inhabits the lowest areas below 400 m. The foothills of the mountains (400–1000 m) present tropical deciduous forest, while the highest areas (1000–2200 m) are occupied by woodlands. The mountains consist of outcrops of plutonic rocks, primarily granite, whereas the foothills and lowlands are composed of alluvial deposits that originated from the same rock formations (León de la Luz & Domínguez-Cadena 1989). The mean rainfall in the lowlands is 200 mm, meanwhile in the highlands it is from 500 to 900 mm. Our sampling was carried out in the lowlands and foothills of the Cape Region (Fig. 1).

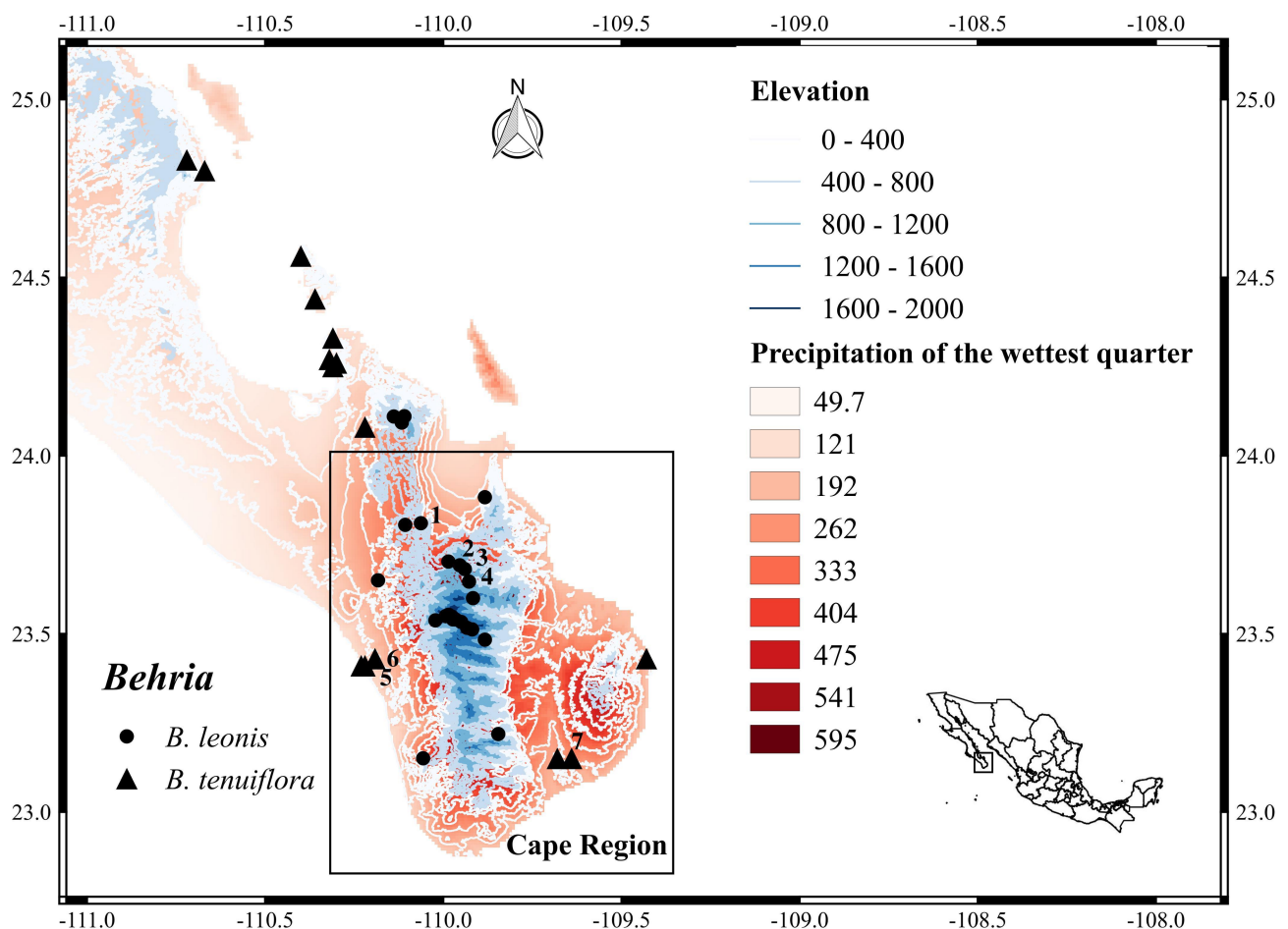


FIGURE 1. Geographic distribution of the genus *Behria*. Black circles = *B. leonis*, black triangles = *B. tenuiflora*. Numbers are populations sampled for both species. Elevation in m and precipitation in mm.

Taxon sampling:—We measured a total of 94 plants obtained from seven populations of *Behria tenuiflora*. The populations were divided into two groups: Group A comprised populations found at lower elevations ranging from 10

to 110 m, while Group B included populations from Sierra de la Laguna, ranging from 400 to 860 m (Table 1 and Fig. 1). Voucher specimens corresponding to the collected and measured plants were deposited at IBUG (acronym follow Thiers 2024). Field trips were conducted in September 2021, covering the documented geographic distribution of *B. tenuiflora* (see Table 1).

TABLE 1. *Behria* populations measured. Specimens were deposited at the IBUG herbarium (acronym based on Thiers 2024).

Population	Species	Longitude	Latitude	Elevation m	Annual precipitation (mm)	Voucher
1	<i>B. leonis</i>	-110.063017	23.810359	435	414	<i>E. Gándara et al. 3298</i>
2	<i>B. leonis</i>	-109.985759	23.702688	690	444	<i>E. Gándara et al. 3299</i>
3	<i>B. leonis</i>	-109.953751	23.692257	853	458	<i>E. Gándara et al. 3300</i>
4	<i>B. leonis</i>	-109.927886	23.646407	811	440	<i>E. Gándara et al. 3301</i>
5	<i>B. tenuiflora</i>	-110.230620	23.4131490	4	134	<i>E. Gándara et al. 3305</i>
6	<i>B. tenuiflora</i>	-110.191888	23.4317630	3	166	<i>E. Gándara et al. 3306</i>
7	<i>B. tenuiflora</i>	-109.640027	23.1540417	110	288	<i>E. Gándara et al. 3307</i>

Morphological characters:—Nine quantitative characters were chosen for analysis (Table 2). The measurements were conducted *in situ*, directly on living plants, using an electronic vernier (Absolute AOS Digimatic, Mitutoyo®) and a metric scale. One flower per plant was measured, with an attempt to measure 10 to 15 flowers in each population. All flower measurements were taken while the plants were alive. In certain cases, flowers were dissected and photographed for further comparisons.

TABLE 2. Morphological characters measured for the *Behria* species/populations/plants.

	Scape length (mm)	Pedice l length (mm)	Perianth length (mm)	Tepal lobes length (mm)	Tepal lobes width (mm)	Perianth opening (mm)	Perianth base joint (mm)	Leaf length (mm)	Leaf width (mm)
<i>Behria leonis</i>									
N	54	54	54	54	54	54	54	54	54
Min	220	13.35	21.93	3.97	3.17	8.55	3.12	130	1.34
Max	690	45.6	32.19	6.73	5.53	14.37	6.44	760	3.33
Mean	410.4	27.2	26.6	5.55	4.13	10.98	4.87	417.7	2.24
S. E.	12.68	0.98	0.28	0.09	0.06	0.16	0.09	19.67	0.05
S. D.	93.21	7.24	2.08	0.67	0.49	1.23	0.67	144.60	0.39
<i>Behria tenuiflora</i>									
N	40	40	40	40	40	40	40	40	40
Min	275	10.94	17.54	1.55	1.73	3.93	4.66	170	1.15
Max	780	46.45	26.58	4.23	3.73	6.29	8	880	2.94
Mean	429.1	22.45	21.25	2.98	2.72	4.78	6.62	410.62	2.14
S. E.	16.93	1.34	0.39	0.08	0.06	0.09	0.14	24.38	0.06
S. D.	107.13	8.53	2.49	0.56	0.42	0.58	0.94	154.22	0.44

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

Morphological analyses:—We conducted a Shapiro-Wilk test to assess the normality of the nine morphological characters selected. Subsequently, a Pearson’s product-moment correlation was performed, and variables exhibiting high correlation ($r > 0.7$) were excluded from the analyses to discard collinearity. The analyses were then conducted using only the remaining parametric variables, namely pedicel length, perianth length, perianth base diameter, and perianth aperture diameter. An Analysis of Variance (ANOVA) was performed on these four characters for each group. Additionally, a Multivariate Analysis of Variance (MANOVA) was conducted to examine if the four characters exhibited similar multivariate means. If the MANOVA indicated a significant overall difference between characters, *post-hoc* pairwise comparisons were performed using Hotelling’s *p*-values. Statistically significant differences were considered for $P < 0.05$.

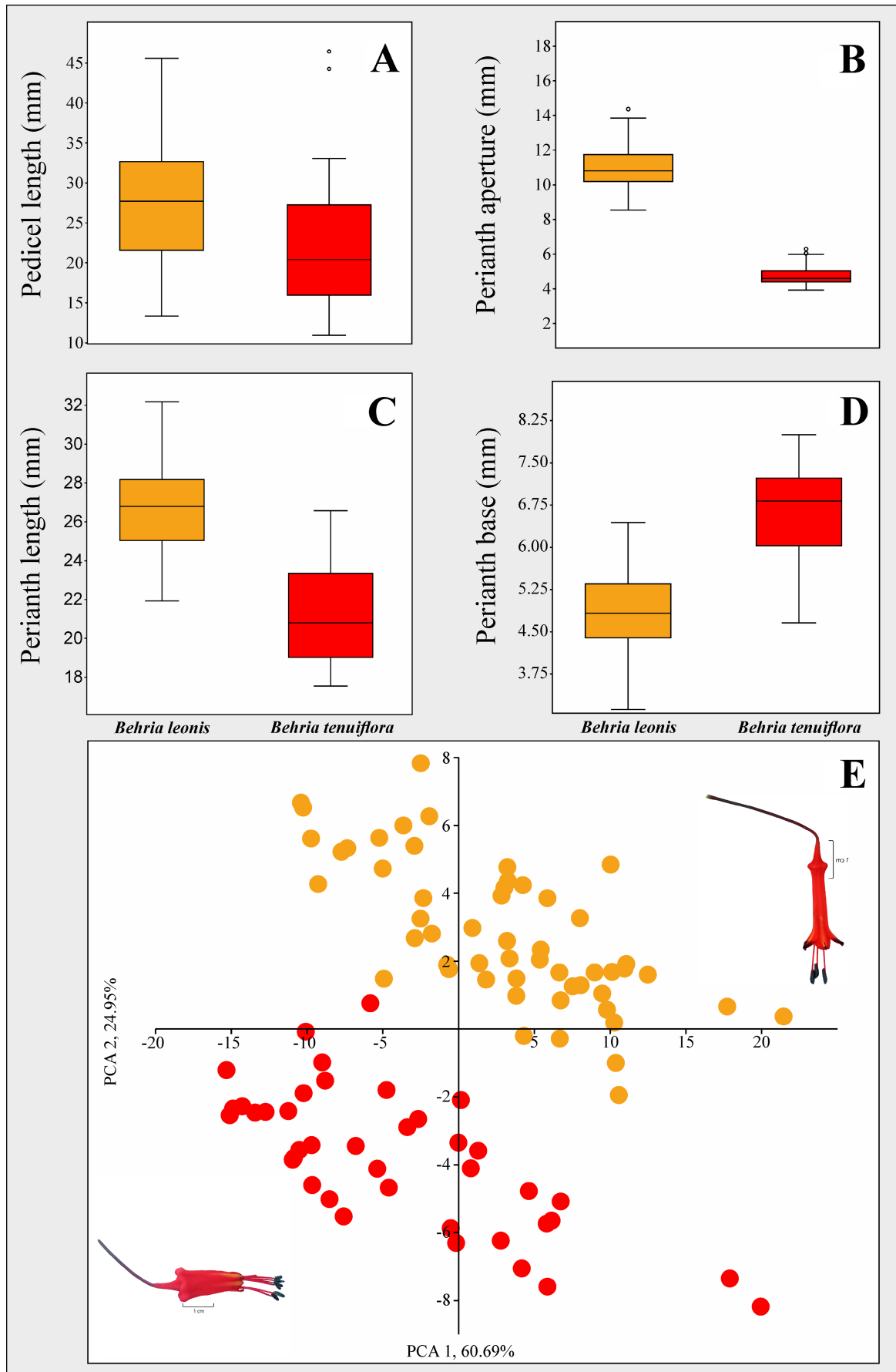


FIGURE 2. Box-plots for four characters that were significantly different among species ($P < 0.05$). A. Pedicel length. B. Perianth aperture. C. Perianth length. D. Perianth base. Boxes represent 75% of the variation and horizontal bars the other 25%; middle lines indicate the median; dots indicate outliers. E. PCA analysis. Red circles = *Behria tenuiflora*, orange circles = *B. leonis*.

To assess the morphological variation between the two *Behria* groups, a principal component analysis (PCA) was employed to examine how the variables explained the data variance. All statistical analyses were carried out using Past v. 4.02 (Hammer *et al.* 2001).

Correlation between climatic variables and morphological variation:—We employed the BEST routine to examine whether the morphological variation between the two sampled groups of *Behria* was correlated with specific climatic conditions. The BEST routine is a test that assesses the extent to which an abiotic data matrix explains a particular biological pattern (Clarke & Gorley 2006). This procedure requires two data subsets, and their construction is described below. For the climatic variables database, we recorded the georeferenced location (latitude, longitude, and elevation) of each of the seven sampled populations (Table 1, Fig. 1). We downloaded the 19 bioclimatic variables from WorldClim (2020). Subsequently, using QGIS 2.16.3 software (QGIS Development Team 2020), we uploaded the coordinates for each locality and the raster files for the 19 bioclimatic variables. The 19 bioclimatic variables were extracted for all localities using the point sampling tool plugin in QGIS 2.16.3. To avoid collinearity among the climatic variables, a PCA was performed in Past v. 4.02 (Hammer *et al.* 2001). The final climatic database consisted of five normalized variables: temperature seasonality (BIO 4), maximum temperature of the warmest month (BIO 5), annual precipitation (BIO 12), precipitation of the wettest quarter (BIO 16, is the wettest quarter of the year and it is determined, to the nearest month, and the total precipitation over this period is calculated), and precipitation of the warmest quarter (BIO 18).

The morphological data encompassed the nine characters listed in Table 2 and the seven sampled populations. To achieve a symmetrical matrix with the climatic database, we calculated the mean of each character per population. The final morphological database was square root transformed and converted into a Bray-Curtis resemblance matrix. Once the two symmetrical data subsets were prepared, a general test using the five climatic variables was conducted. This allowed us to identify the optimal combination of climatic variables that correlated with the morphological variation. Subsequently, pairwise comparisons were performed between each selected combination to assess the significance of the test.

Conservation status:—To assess the species risk of extinction, we calculated two parameters proposed by the IUCN Red List of Threatened Species (IUCN, 2024). We employed occurrence records to evaluate the extent of occurrence (EOO) and the area of occupancy (AOO). The EOO was determined by employing a convex polygon method, while the AOO was calculated using a 2×2 km grid cell. The estimation of both EOO and AOO was performed using GeoCat (Bachman *et al.* 2011).

Results

Morphological analyses:—Summary statistics for all morphological variables can be found in Table 2 and Appendix S1. The ANOVA revealed statistically significant differences ($P < 0.05$) in pedicel length, perianth length, perianth base diameter, and perianth aperture diameter (Table 3) between Group A and Group B.

The overall MANOVA analysis demonstrated significant differences among the four characters ($F = 363.5$, $P < 0.0001$). Pairwise comparisons between the two groups showed significant differences ($P < 0.0001$) (Table 3).

The PCA based on four morphological variables found that the two first components (PC1 = 79%; PC2 = 16.86%) explained almost 95% of the variation. Table 3 shows that pedicel length loaded positively on PC1, while perianth length and perianth opening loaded positively on PC2. The PCA displayed two distinct, non-overlapping groups.

Correlation between climatic variables and morphological variation:—The overall BEST routine, which involved the five climatic variables and the morphological variables, revealed significant differences ($Rho = 0.851$, $P < 0.001$). Among all the possible combinations tested, three climatic variables showed high and significant correlations with the morphological characters (Table 4). The precipitation of the wettest quarter emerged as the most influential variable since it was part of every significant combination and exhibited a strong correlation ($Rho = 0.84$, $P < 0.001$) with the morphological variation on its own. Interestingly, all the combinations with the highest correlation values involved variables related to precipitation. It is noteworthy that the annual precipitation in the *Behria* populations of Sierra de La Laguna was more than double compared to the other populations (Table 1).

Given the statistically significant morphological differences observed among the analyzed *Behria* populations, we propose the recognition of a new taxon and proceed to discuss its implications.

TABLE 3. ANOVA, MANOVA and PCA loadings results.

ANOVA					
	Sum of sqrs	df	Mean square	F	p (same)
Pediceal					
Between groups:	521.682	1	521.682	8.539	0.004373
Perianth					
Between groups:	668.294	1	668.294	129.8	2.85E-19
Perianth opening					
Between groups:	884.5	1	884.5	867.6	1.26E-48
Perianth base					
Between groups:	70.0012	1	70.0012	109.9	2.20E-17
MANOVA					
Wilks' lambda:	0.05768				
df1:	4				
df2:	89				
F:	363.5				
p (same):	3.16E-54				
PCA loadings					
	PC 1	PC 2	PC 3	PC 4	
Pediceal	0.95271	-0.29631	-0.056494	-0.03693	
Perianth	0.24554	0.64889	0.71966	0.027062	
Perianth opening	0.17821	0.66986	-0.67436	0.2545	
Perianth base	-0.017408	-0.20599	0.15535	0.96599	

TABLE 4. BioEnv results. Bold numbers indicate significant results.

Number of variables	Rho value	P value	Variables combination
2	0.851	<0.001	Annual precipitation + Precipitation of wettest quarter
1	0.847	<0.001	Precipitation of wettest quarter
3	0.842	<0.001	Annual precipitation + Precipitation of wettest quarter + Precipitation of Warmest Quarter

Taxonomic treatment

Morphological key to *Behria* and *Bessera* species

1. Flowers tubular, gamopetalous; staminal tube absent2
1. Flowers campanulate, dialypetalous; staminal tube present.....3
2. Corms 31–45 mm in length; flowers tubular; perianth prominently saccate at the junction of the tube and ovary; growing on lowland areas (10–150 m) *Behria tenuiflora*
2. Corms 11.3–31 mm in length; flowers hypocrateriform; perianth slightly saccate at the base; growin on mid-to-high elevation areas (400–2060 m) *Behria leonis*
3. Tepals pinkish to light lilac; filaments forming a staminal tube 1–2 mm long; endemic to Sierra de El Cuale, Jalisco *Bessera tuitensis*
3. Tepals carmine, scarlet, light red, violet, purplish or fuchsia; filaments forming a tube 7.5–17 mm long; widely distributed.....4
4. Staminal tube dark purple, conical; filaments dark purple, cuneate and flattened..... *Bessera ramirezii*
4. Staminal tube white, whitish or violet, cylindrical; filaments scarlet, red, violet or purple, terete or semiterete.....5
5. Tepals carmine, ruby or red; staminal tube white or whitish, 7.5–16.5 mm long; filaments carmine, ruby, red or violet, terete, 7.8–21.7 mm long; from Balsas Basin, Chihuahuan Desert, Sierra Madre Occidental, Sierra Madre del Sur and Transmexican Volcanic Belt..... *Bessera elegans*
5. Tepals light red, scarlet, violet, magenta or fuchsia; staminal tube whitish or violet, 7.5–13.2 mm long; filaments violet or purple, semiterete, 5.3–10.2 mm long; from Pacific Lowlands..... *Bessera elegantissima*

Behria leonis E. Gándara & Ruiz-Sanchez *sp. nov.*, Figs 3–4.

TYPE:—MEXICO. Baja California Sur: Municipio, La Paz, Sierra de La Laguna, Km 11 brecha a Termopilas, Ejido San Antonio, adelante de San José del Rancho, 23.702688, -109.985759, elevation 690 m, 23 September 2021, deciduous tropical forests, E. Gándara *et al.* 3299 (holotype IBUG!).

Behria leonis differs from *B. tenuifolia* in having a longer perianth (2.2–3.2 cm vs. 1.7–2.6 cm), a wider perianth aperture (8.5–14.3 mm vs. 3.1–6.4 mm), a narrower perianth base (3.9–6.3 mm vs. 4.6–8 mm), hypocrateriform flowers instead of tubular flowers, and perianth slightly saccate at the base vs. perianth prominently saccate.

Perennial herbs, geophytes. *Roots* fibrous. *Corms* 13.2–29.2 mm in diameter, 11.3–31 mm long, subglobose with brownish membranous cataphylls. *Leaves* (1–)2–4(–6), 13–76 × 1.3–3.3 cm, linear, fistulose, with longitudinal striae, glabrous to minutely hispidulous, rounded and hollow in transversal section, green. *Scapes* 22–69 cm long, glabrous to minutely denticulated, cylindrical in transverse section (in fresh specimens), green, sometimes purplish at base or at apex. *Inflorescences* umbellated with spathe bracts 3–6, 2–6 mm long, membranaceous, greenish to purplish becoming hyaline. *Flowers* (2–)5–18(–23), pedicels 1.3–4.5 cm long; pendulous turning erect after anthesis, green to purplish; perianth 2.2–3.2 cm long, slightly saccate at the base, hypocrateriform, tepals with 6 lobes 3.9–6.7 mm long, 3.1–5.3 mm wide, forming a tube but with free apex forming a wide perianth aperture, red with a yellow band from apex to the middle in the external side of the lobes, and from the apex to the base in the internal side of the lobes, with the apex turning purple to blackish; stamens 6, exerted in mature flowers, joined solely at base for <1 mm, a staminal ring or staminal tube is absent; filaments (20–)21–30.5(–32) mm long after anthesis, cylindrical, pale reddish to magenta, sometimes becoming withish at the base; anthers (1.5–)2–4(–4.3) mm long, 0.5–0.8 mm wide after anthesis, ellipsoid, dorsifixed with longitudinal dehiscence, black before anthesis, turning grayish or greenish after anthesis, sometimes bluish or greenish in dried specimens; ovary (3.8–)4.2–7(–8.2) mm long, ellipsoid, trilobulated; disposed on a gynophore (0.8–)1.5–3.5(–4.5) mm long, green; style 15.5–29.4(–31) mm long, cylindrical, reddish to magenta; stigma trilobed, magenta to purplish with white trichomes. *Fruits* a capsule 9–14 mm long, trilobulated, loculicide. *Seeds* (5–)7–9(–11) mm long, irregularly lenticular, flattened, minutely granular, black.

Distribution, habitat and phenology:—*Behria leonis* is distributed along Sierra de la Laguna from 400 to 2060 m (Fig. 1). This species inhabits the tropical deciduous forest and oak-pine forest (León de la Luz *et al.* 2000). In the Cape Region, sandy soils, derived from granitic rocks prevail, fostering the formation of deep soils conducive to the growth of corms in this species (León de la Luz *per. com.*). Flowering records of *B. leonis* indicate that this species flowers from August to November, while fruits are recorded from September to December. Arriaga *et al.* (1990) mentioned that *B. leonis* is part of the plants that *Hylocharis xantusii* forage looking for nectar, we saw this endemic species of hummingbird and *Phoebis sennae* butterflies visiting the flowers during our field work (Fig. 4 A).

Etymology:—The species epithet “*leonis*” is named in honor of the Mexican botanist José Luis León de la Luz. He is a highly regarded researcher who retired from CIBNOR (Centro de Investigaciones Biológicas del Noroeste S.C.) and is known as the foremost botanist in Southern Baja California Sur. Throughout his career, José Luis León de la Luz has extensively collected thousands of plants in the region and has made significant contributions to the field of botany. Notably, he played a role in neotypifying *Behria tenuiflora*, ensuring a standardized reference specimen for future studies. Furthermore, he collaborated on projects involving the extraction and identification of alkaloids from this species, contributing to the understanding of its chemical composition.

Conservation status:—The calculated EOO for *Behria leonis* was 2612 km², while the AOO was 72 km². Based on the results of the analysis of the extent of occurrence (EOO) and area of occupancy (AOO), *B. leonis* meets the criteria B1ab(i)+2ab(ii) (B = Geographic range in the form either EOO and/or AOO). Based on these values and the corresponding criteria, *B. leonis* should be classified as Endangered (EN) according to the IUCN Red List Categories and Criteria (IUCN 2024). This classification indicates that the species will face a high risk of extinction in the wild if conservation measures are not implemented. However, populations of this species in the high mountains, up to 1000 m of elevation, are healthy, dense, and free of human threats (León de la Luz *pers. com.*).

Additional specimens examined (paratypes):—MEXICO. Baja California Sur: Los Cabos, eastern foothills of the Sierra de la Laguna, 12.5 km west of MEX 1 along the road to San Pedro de la Soledad, 23.21861, -109.845833, elevation ca. 950 m, 5 November 1997, V. Steinman & T. LaDoux 1274 (MEXU); Campamento de Palo Extraño, 23.516667 -109.933333, elevation 1780 m, 9 September 1986, R. Domínguez Cadena 270, 270a (HCIB); Cañón de La Zorra, abajo de San Juanito, 23.512282 -109.919107, elevation 1550 m, 30 October 1979, J.L. León de la Luz 122 (HCIB); Paso de Golondrinas, al SE del Campamento Palo Extraño, 23.483333 -109.883333, elevation 1900 m, 1 November 1985, R. Domínguez Cadena 113 (HCIB); Ca. del Rancho La Victoria, 23.6 -109.916667, elevation 1600

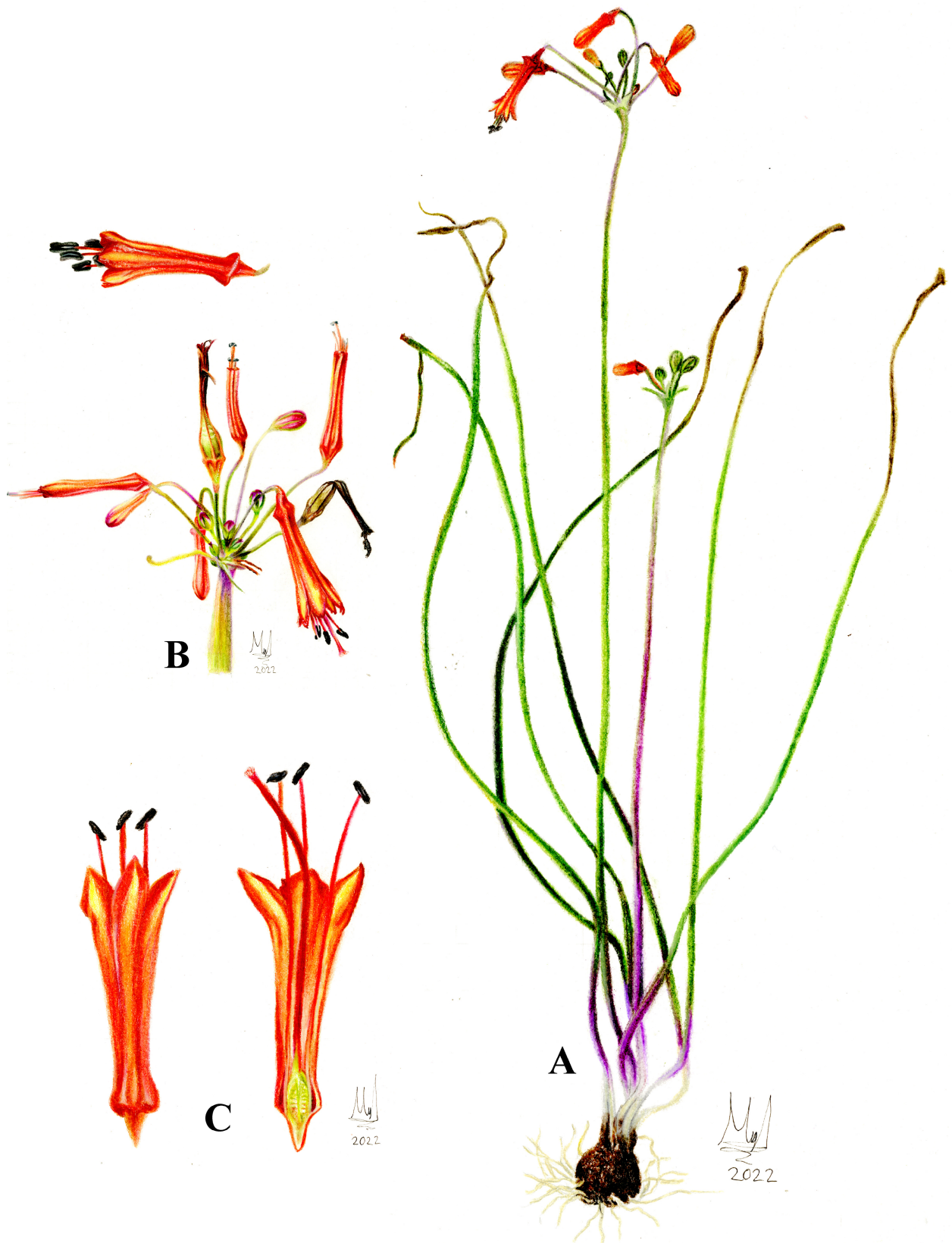


FIGURE 3. *Behria leonis*. A. Complete plant with corms, leaves, inflorescence and flowers. B. Inflorescence, flowers and fruits. C. Dissected flower, external and internal views. Illustration by Miguel Jiménez, based on *E. Gándara et al.* 3298.



FIGURE 4. *Behria leonis* (A, C, E), *B. tenuiflora* (B, D, F). A. Butterfly (*Phoebis sennae*) visiting flowers. B. Inflorescence view. C. Close up to hypocotyl flowers. D. Close up to tubular flowers. E- F. Dissected flowers, external and internal views.

m, 30 September 1994, *M. Domínguez León* 797 (HCIB); Ca. Rancho Matancitas, 23.150408 -110.056625, elevation 400 m, 30 October 1987, *J.L. León de la Luz* 3042 (HCIB), Ca. Rancho Matancitas, 23.150408 -110.056625, elevation 400 m, 23 October 1987, *R. Domínguez Cadena* 644 (HCIB). La Paz, Rancho Laguna and vicinity, Sierra Laguna, Cape District, elevation 1670–1830 m, 3 October 1951, *H. S. Gentry* 11214 (MEXU); granitic slopes surrounding long interior valley (La Laguna), south of Pico La Aguja on Sierra de la Laguna, elevation 1920–2040 m, 22 October 1977, *D.E. Breedlove & D.I. Axelrod* 43363 (MEXU); Sierra de la Laguna, ca. de la Cieneguita del Picacho, 23.549548, -109.993299, elevation 1846 m, 2 September 2008, *J.L. León de la Luz* 2008-130 (HCIB), Sierra de La Laguna, Camino de El Triunfo a San Antonio, 23810359, -110063017, elevation 435 m, 23 September 2021, deciduous tropical forests with xerophilous elements, *E. Gándara, E. Ruiz & M. Gómez* 3298 (IBUG!); Sierra de La Laguna, Km 15 brecha a Termopilas, Ejido San Antonio, 23692257, -109953751, elevation 853 m, 23 September 2021, deciduous tropical forests, *E. Gándara, E. Ruiz & M. Gómez* 3300 (IBUG!); Sierra de La Laguna, Km 21 brecha a Termopilas, 23646407, -109927886, elevation 811 m, 23 September 2021, deciduous tropical forests, *E. Gándara, E. Ruiz & M. Gómez* 3301 (IBUG!); Sierra de La Laguna, Cerro San Antonio al E del Valle La Laguna, 23.540374 -109.973173, elevation 1985 m, 21 October 1987, *J.L. León de la Luz* 2930, 2932 (HCIB); Bajada al Rancho La Burrera, 23.537604 -110.022257, elevation 1135 m, 2 November 1985, *J.L. León de la Luz* 925 (HCIB); Arroyo de Los Encinos Blancos, 1 km al N del Campamento Forestal, 23.553328 -109.985215, elevation 1754 m, 12 October 1984, *J.L. León de la Luz* 621 (HCIB); Cerro de San Antonio, 23.540498 -109.966092, elevation 1935 m, 13 October 1984, *J.L. León de la Luz* 663 (HCIB); Agua de San Antonio, 23.55 -109.983333, elevation 1920 m, 31 October 1985, *R. Domínguez Cadena* 55 (HCIB); El Barrito, Rancho La Burrera, 25 km al NE de Todos Santos, 23.5 -110.033333, elevation 600 m, 13 September 1994, *M. Domínguez León* 766 (HCIB); Rancho El León, 23.681566 -109.939772, elevation 860 m, 4 September 1998, *J.L. León de la Luz* 9190 (ARIZ, HCIB); Arroyo del Rancho San Antonio de La Sierra, 23.883333 -109.883333, elevation 700 m, 4 September 1998, *M. Domínguez León* 2557 (HCIB); Valle de La Laguna, 23.54799 -109.97546, elevation 1736 m, 30 September 1998, *M. Domínguez León* 2635 (HCIB); Cima del Cerro de San Antonio, 23.533333 -109.95, elevation 2060 m, 14 de September 1999, *M. Domínguez León* 2733 (HCIB); Valle de La Laguna, 23.544259 -109.973038, elevation 1820 m, 27 September 2000, *J.L. León de la Luz* 9703 (HCIB); 1 km al S del Rancho San Antonio de La Sierra, 23.65 -110.183333, elevation 600 m, 7 September 2000, *J.J. Pérez Navarro* 1408 (HCIB); Portezuelo de Los Encinos, Camino al Cerro Puesto de Los Soldados, 24.092791 -110.116676, elevation 922 m, 18 November 2010, *M. Domínguez León* 4774 (HCIB); La Laguna, Sierra de La Laguna. Growing in shade of pine-oak forest, 23.54863 -109.97716, elevation 1675 m, 31 August 1971, *R.R. Snelling* s.n. (SD); Sierra de la Laguna, NE of Todos Santos, vicinity of Valle La Laguna at top of the Sierra, NE of Cañon La Burrera and Rancho Corral Grande, 23.55056 -109.98306, elevation 1740 m, 29 October 1998, *J. Rebman* 5790 (SD, UCR); Sierra Cacachilas, SE of La Paz & W of El Sargento, N of Hwy 286 between La Paz & San Juan de Los Planes, on the top of Cerro El Llano, 24.11067 -110.10963, elevation 1120 m, 29 October 2013, *J. Rebman* 27271 (SD); Sierra las Cacachilas, North of Hwy. 286 between La Paz & San Juan de los Planes, West of El Sargento, on the top of Cerro Morro to the north of El Picacho, 24.10987 -110.13902, elevation 1192 m, 18 October 2014, *J. Rebman* 29067 (SD); Sierra las Cacachilas, north of Hwy. 286 between La Paz & San Juan de los Planes, west of El Sargento, on top of Cerro El Llano (El Tinaja) on the flats & slopes around the base camp, 24.11028 -110.10925, elevation 1120 m, 14 October 2014, *J. Rebman* 28970 (SD); Triunfo, 23.80565 -110.10698, 23 October 1941, *F.F. Gander* 9736 (SD); Sierra de la Laguna, rancho San Antonio de la Sierra, 11.6 miles SE of KP 147.6 (Hwy. 1), elevation 3000 ft, 11-12 September 1985, *J. Donahue* 97.169 (GA); rancho Termopilas, km 16 de brecha a San Antonio de la Sierra, Sierra de la Laguna, 23.685353 -109.992381, elevation 807 m, 14 septiembre 2021, *M. Anguiano, D. Anguiano & R. Domínguez* 902 (IBUG).

Discussion

We have identified significant morphological and climatic differences that distinguish *Behria leonis* (*B. tenuiflora* Group B) as a separate species from *Behria tenuiflora* (Group A). In his study, Moore (1953) also recognized two distinct groups within *B. tenuiflora* based on variations in flower characteristics. Group A, representing *B. tenuiflora*, exhibits a smaller perianth (18–22 mm long) with a prominently saccate base, as well as narrower lobes (2–4 mm long and 1–2 mm wide). Our findings align with these measurements, as shown in Table 2. Group B (*Behria leonis*) displays a larger perianth (25–32 mm long) a slightly saccate base, and both longer and wider lobes measuring (3–)4–7 mm long and 3–5 mm wide (Moore 1953). Once again, our results from Table 2 coincide with these measurements. While Moore (1953) did not explicitly mention the floral form, he provided illustrations of both morphotypes in his

figures [specifically, Moore's figure 107 A (Ac for *B. tenuiflora*) and A (Ab for *B. leonis*)]. It is worth noting that *B. tenuiflora* possesses tubular flowers, while *B. leonis* exhibits hypocrateriform flowers, as depicted in Figure 4.

Romero-Schmidt *et al.* (1995) conducted a morphometric study on three populations of *Behria tenuiflora* located at La Laguna, Matancitas, and Pichilingue localities. They measured 14 morphological characteristics in a total of 90 individuals. Their findings indicated that the population from Sierra de La Laguna exhibited distinct differences compared to the other two populations. In our study, we did not measure individuals from Matancitas and Pichilingue due to their sterile state at the time of the research. However, we reviewed herbarium specimens from these areas and those agree with our results. These findings indicate consistency with their conclusions that the three populations represent different ecotypes of *B. tenuiflora*. Romero-Schmidt *et al.* (1995) also suggested the possibility of a subspeciation process occurring among these three ecotypes. However, based on our results, we assert that the populations from La Laguna should not be considered a subspecies but rather a distinct species of *B. tenuiflora*.

Romero-Schmidt *et al.* (1995) made an interesting observation regarding the flowering patterns of different populations. They noted that individuals from La Laguna appear annually, whereas those from Pichilingue appear once every three years. Additionally, as stated in Table 1, the populations of *Behria leonis* experience approximately twice as much annual precipitation compared to those of *B. tenuiflora*. This difference in precipitation could potentially explain why *B. tenuiflora* populations flower every three years, while *B. leonis* populations flower annually, as stated by Romero-Schmidt *et al.* (1995).

Climate factors are crucial in shaping floral morphology (Campbell & Powers 2015). Our study revealed that precipitation during the wettest quarter of the year stood out as the most significant climatic factor linked to morphological variation between groups A and B. This aligns with the overall annual precipitation, which notably differs across the habitats of the two species. Previous research has also identified precipitation as a key factor driving morphological differences in *Bessera* (Gándara *et al.* 2021). These precipitation variables contribute to the observed morphological differences between the two *Behria* species and may contribute to ecological isolation, as observed in other studies (Weber *et al.* 2020). For instance, Rodríguez-Peña & Wolfe (2023) discovered a strong correlation between mean annual precipitation and flower morphology in *Penstemon glandulosus* Douglas ex Lindley (1829: 1262). Our findings align with a study on an Apiaceae genus in the Atacama Desert by Padin & Calviño (2023), where precipitation along a latitudinal gradient drove the separation of two morphotypes and contributed to the diversification of *Eryngium anomalum* Hooker & Arnot in Hooker (1833: 350) and *E. atacamense* Padin & Calviño (2023: 202). Similarly, we observed comparable results but within an altitudinal gradient in the Cape Region. The authors also noted that *Eryngium* Linnaeus (1753: 232) species in the Atacama region underwent diversification during the Pliocene-Pleistocene aridification event, akin to the *Behria* clade (Gándara *et al.* 2014). Confirming the stability of these morphotypes under controlled temperature and precipitation conditions through common garden experiments is a possibility. However, in 2007, we collected corms of a "morphotype" of *Bessera elegans*, now recognized as *Bessera ramirezii* (Gándara *et al.* 2021), in Colima and transplanted them to a greenhouse in Xalapa. Every blooming season, the individuals displayed their morphotypes from Colima. Further testing and research are imperative to fully grasp the extent of climate's influence on the floral morphology of this group.

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Appendix S1. Morphological characters measured for the *Behria* species/populations/plants.

Species	Population No.	Scape length (mm)	Pedicle length (mm)	Perianth length (mm)	Tepal lobes length (mm)	Tepal lobes width (mm)	Perianth opening (mm)	Perianth base joint (mm)	Leaf length (mm)	Leaf width (mm)
<i>B. leonis</i>	1	360	33,9	27,82	5,47	5,53	400	3,07	10,05	4,46
<i>B. leonis</i>	1	415	21,28	29,96	5,52	4,05	430	2,26	10,68	6,05
<i>B. leonis</i>	1	480	36,53	29,05	6,29	4,4	510	2,42	11,34	6,05
<i>B. leonis</i>	1	380	35,11	29,17	4,06	4,47	690	2,49	10,69	4,84
<i>B. leonis</i>	1	330	20,75	27,83	5,23	4,12	315	2,22	10,83	4,82
<i>B. leonis</i>	1	420	29,62	27,92	5,24	3,79	385	2,34	12,63	5,69
<i>B. leonis</i>	1	325	27,98	27,98	6,16	4,29	350	2,81	12,11	4,68
<i>B. leonis</i>	1	410	29,58	28,02	6,41	4,49	440	2,04	10,22	5,59
<i>B. leonis</i>	1	455	31,82	28,16	6,3	4,31	315	2,31	12,56	5,9
<i>B. leonis</i>	1	295	21,75	27,63	5,31	3,35	210	1,65	9	4,28
<i>B. leonis</i>	1	550	20,19	32,19	6,07	4,15	430	2,62	10,24	5,62
<i>B. leonis</i>	1	360	45,6	28,48	5,51	4,21	510	2,51	13,85	5,36
<i>B. leonis</i>	1	565	33,2	28,22	4,68	3,59	470	2,77	10,51	5,22
<i>B. leonis</i>	1	400	18,95	27,14	5,33	3,57	255	2,26	9,65	4,64
<i>B. leonis</i>	1	510	34,24	28,6	3,97	3,42	500	3,33	11	6,44
<i>B. leonis</i>	2	360	25,08	28,22	5,13	4,46	370	2,23	8,55	4,16
<i>B. leonis</i>	2	410	34,97	26,18	4,54	4,5	310	2,22	11,13	5,44
<i>B. leonis</i>	2	460	26,95	28,66	6,23	5,21	500	2,11	11,14	4,57
<i>B. leonis</i>	2	410	35,98	24,63	5,71	3,67	370	2,18	9,42	3,91
<i>B. leonis</i>	2	428	21,67	24,97	5,21	3,45	495	3,02	10	5
<i>B. leonis</i>	2	515	26,52	25,65	6,35	3,77	445	2,05	9,49	4,43
<i>B. leonis</i>	2	485	23,95	25,31	6,14	4,43	760	2,43	9,24	4,13
<i>B. leonis</i>	2	420	32,5	27,01	5,06	3,25	380	2,32	10,73	4,96
<i>B. leonis</i>	2	355	24,16	24,36	4,5	3,71	420	2,41	10,09	4,23
<i>B. leonis</i>	2	490	35,12	27,86	5,57	3,92	470	3	11,72	4,72
<i>B. leonis</i>	2	440	27,84	26,17	5,91	3,99	570	2,07	10,36	3,99
<i>B. leonis</i>	3	420	13,42	26,63	6,41	4,1	340	1,95	10,46	4,89
<i>B. leonis</i>	3	420	41,9	28,39	6,45	4,92	380	1,99	12,93	5,99
<i>B. leonis</i>	3	305	20,2	24,31	6,22	4,71	330	2,09	14,37	3,12
<i>B. leonis</i>	3	310	16,62	25,37	6,42	4,38	280	1,76	11,48	5,46
<i>B. leonis</i>	3	400	22,72	25,06	4,39	3,56	650	2,23	10,6	5,07
<i>B. leonis</i>	3	280	28,57	25,66	4,89	4,35	190	1,9	9,72	4,59
<i>B. leonis</i>	3	360	27,58	25,32	5,66	4,09	370	1,99	12,05	4,66
<i>B. leonis</i>	3	270	31,5	24,58	5,2	4,57	440	2,36	12	5,03
<i>B. leonis</i>	3	400	26,61	29,44	5,47	4,19	280	2,2	9,47	4,17
<i>B. leonis</i>	3	310	16,2	26,71	5,57	3,88	290	2,13	9,68	4,95
<i>B. leonis</i>	3	290	26,83	27,33	6,09	4,21	250	1,6	12,43	5,7
<i>B. leonis</i>	3	370	14,17	26,31	6,12	4,1	245	2,25	9,86	5,3
<i>B. leonis</i>	3	290	20,23	21,93	4,61	3,92	130	1,63	10,41	4,62
<i>B. leonis</i>	3	340	18,47	27,19	5,88	3,8	290	2,31	10,91	5,2
<i>B. leonis</i>	3	280	15,22	23,44	4,83	4,25	250	1,92	10,7	3,99
<i>B. leonis</i>	4	580	31,86	23,23	4,86	4,29	650	1,9	11,55	4,27
<i>B. leonis</i>	4	450	29,9	24,44	6,36	3,63	430	2,63	12,95	4,16
<i>B. leonis</i>	4	520	31,03	27,29	5,05	3,17	600	2,24	10,25	4,57
<i>B. leonis</i>	4	690	28,45	25,25	5,57	3,97	525	1,93	11,06	5,34
<i>B. leonis</i>	4	500	26,01	24,88	5,46	4,3	635	2,29	10,79	4,62
<i>B. leonis</i>	4	530	32,1	26,11	5,77	4,92	570	2,28	11,07	3,96
<i>B. leonis</i>	4	220	34,36	26,89	5,66	3,64	255	1,62	10,71	5,35
<i>B. leonis</i>	4	380	13,35	25,3	5,61	4,1	180	1,34	11,82	4,54

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Appendix S1 (Continued)

Species	Population No.	Scape length (mm)	Pedicel length (mm)	Perianth length (mm)	Tepal lobes length (mm)	Tepal lobes width (mm)	Perianth opening (mm)	Perianth base joint (mm)	Leaf length (mm)	Leaf width (mm)
<i>B. leonis</i>	4	500	35,51	24,65	5,57	3,9	660	2,89	10,88	4,79
<i>B. leonis</i>	4	460	26,75	29,23	6,62	4,7	540	2,23	11,27	5,08
<i>B. leonis</i>	4	400	29,58	22,08	5,79	4,86	540	1,87	12,14	5,46
<i>B. leonis</i>	4	530	33,27	30,06	6,73	4,9	590	2,42	13,54	5,33
<i>B. leonis</i>	4	330	21,96	24,54	4,62	3,76	370	1,89	11,06	3,88
<i>B. tenuiflora</i>	5	385	13,74	19,67	2,55	2,88	210	2,11	4,65	7,16
<i>B. tenuiflora</i>	5	360	10,94	20,04	3,46	3,59	260	1,46	4,54	6,03
<i>B. tenuiflora</i>	5	410	11,55	18,6	2,96	2,94	320	2,04	4,54	7,08
<i>B. tenuiflora</i>	5	375	16,78	22,85	3,03	2,75	440	1,84	4,95	6,71
<i>B. tenuiflora</i>	5	280	18,61	18,14	3,38	2,44	285	1,66	4,38	6,96
<i>B. tenuiflora</i>	5	455	21,34	19,21	4,23	3,73	400	2,16	6,05	7,48
<i>B. tenuiflora</i>	5	355	19,71	17,54	3,2	3,15	400	2,13	4,51	6,38
<i>B. tenuiflora</i>	5	320	21,03	23,56	3,21	2,75	430	1,97	5,14	7,4
<i>B. tenuiflora</i>	5	285	17,34	18,37	3,55	3,34	180	2,04	4,54	8
<i>B. tenuiflora</i>	5	380	15,19	19,24	3	3,06	390	2,36	5,99	7,97
<i>B. tenuiflora</i>	6	420	26,42	20,39	1,74	2,55	385	2,77	4,46	7,23
<i>B. tenuiflora</i>	6	420	16,29	19,04	3,03	2,41	320	2,09	4,23	5,59
<i>B. tenuiflora</i>	6	610	27,04	19,02	3,35	2,52	415	1,98	4,83	5,33
<i>B. tenuiflora</i>	6	510	15,98	18,72	2,48	2,59	730	2,86	4,43	6,85
<i>B. tenuiflora</i>	6	275	19,22	26,58	3,23	2,9	230	1,86	4,39	4,66
<i>B. tenuiflora</i>	6	280	12,37	18,66	2,45	2,02	270	1,15	4,52	4,74
<i>B. tenuiflora</i>	6	430	17,25	21,87	3,33	2,21	560	2,38	4,68	4,68
<i>B. tenuiflora</i>	6	335	15,46	24,04	3,52	3,1	370	1,75	4,19	5,49
<i>B. tenuiflora</i>	6	445	15,93	21,09	2,22	2,76	265	1,59	5,07	7,18
<i>B. tenuiflora</i>	6	300	11,72	18,78	1,55	2,01	290	1,96	4,61	6,67
<i>B. tenuiflora</i>	6	340	15,96	18,41	2	2,09	350	1,15	4,49	6,32
<i>B. tenuiflora</i>	6	585	22,27	19,83	3,03	2,94	230	2,49	4,24	4,91
<i>B. tenuiflora</i>	6	416	16,97	19,79	2,96	1,73	355	1,39	4,15	6,03
<i>B. tenuiflora</i>	6	485	13,18	18,69	2,72	2,49	400	2,56	4,97	6,02
<i>B. tenuiflora</i>	6	485	19,8	19,21	3,3	3,07	400	2,03	6,29	7,21
<i>B. tenuiflora</i>	7	445	23,31	23,25	2,83	3,13	640	2,94	5,07	7,07
<i>B. tenuiflora</i>	7	570	27,34	24,04	2,16	2,46	510	2,77	4,64	6,9
<i>B. tenuiflora</i>	7	530	22,7	23,38	3,2	2,49	480	2,21	4,04	6,17
<i>B. tenuiflora</i>	7	490	46,45	25,75	2,71	2,6	510	2,75	4,82	7,68
<i>B. tenuiflora</i>	7	360	33,02	23,94	2,49	2,57	300	2,43	4,96	6,71
<i>B. tenuiflora</i>	7	465	44,26	26,18	3,1	2,47	430	2,29	4,4	6,8
<i>B. tenuiflora</i>	7	780	29,62	21,8	3,28	2,68	880	2,73	3,93	7,13
<i>B. tenuiflora</i>	7	540	27,05	23,15	2,93	3,1	740	2,36	4,7	7,23
<i>B. tenuiflora</i>	7	450	32,68	22,17	3,36	2,62	580	2,44	5,92	7,49
<i>B. tenuiflora</i>	7	475	31,18	21,23	2,32	2,66	460	2,1	4,22	7,99
<i>B. tenuiflora</i>	7	340	32,38	22,32	3,44	3,21	170	2,35	5,5	7,46
<i>B. tenuiflora</i>	7	320	30,95	22,73	3,44	3,33	460	2,48	5,99	7,74
<i>B. tenuiflora</i>	7	570	25,81	24,86	3,18	2,53	500	2,01	5,23	6,34
<i>B. tenuiflora</i>	7	390	33,06	20,52	3,91	2,44	480	2,3	4,53	6,67
<i>B. tenuiflora</i>	7	500	26,11	23,41	3,63	2,65	400	1,85	4,59	5,37

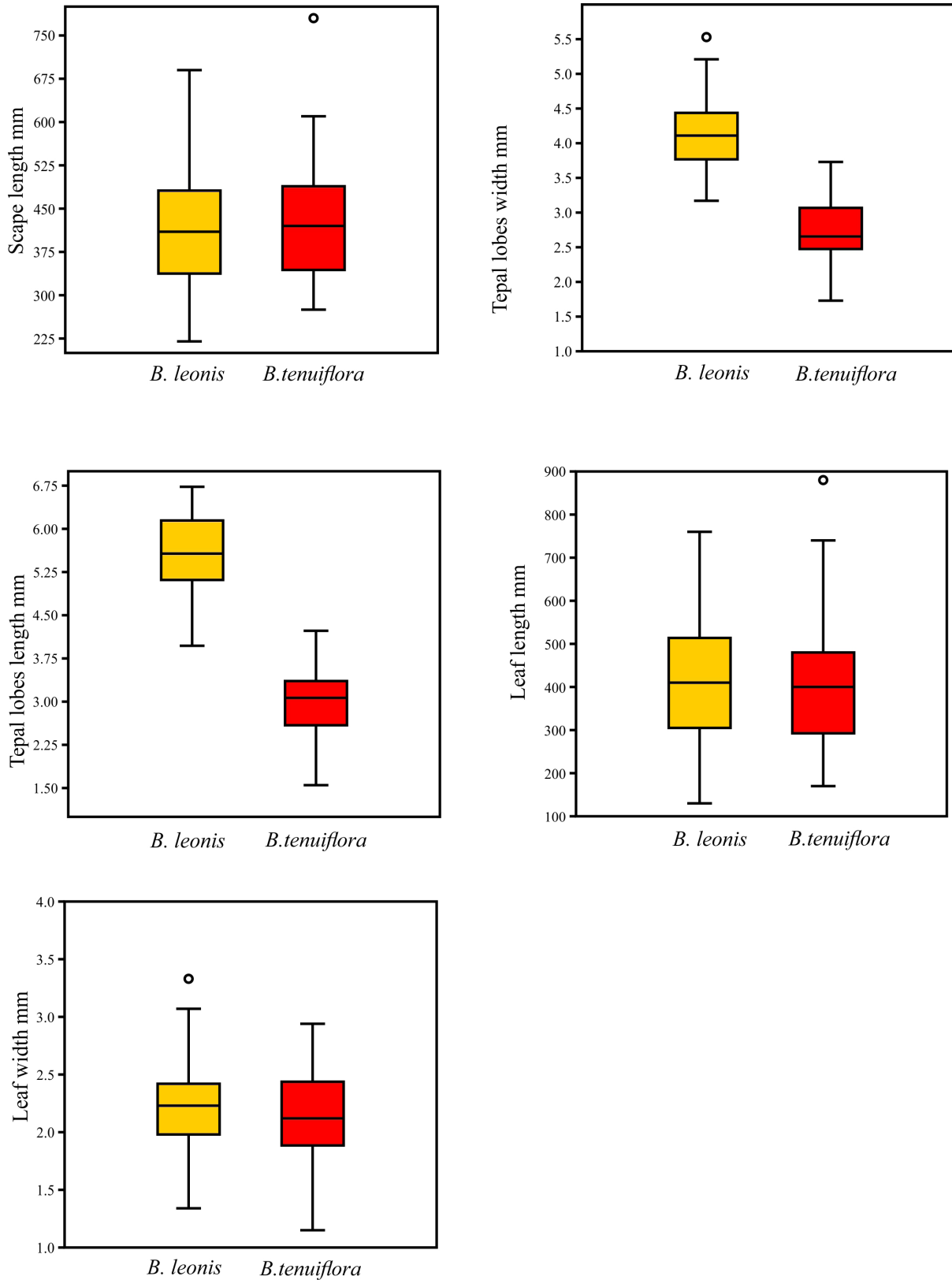


FIGURE S1. Box plots depicting five measured characters for both *Behria* species. Scape length, tepal lobes length, tepal lobes width, leaf length, and leaf width. Boxes represent 75% of the variation and horizontal bars the other 25%; middle lines indicate the median; dots indicate outliers.