PhytoKeys 75: 1–12 (2016) doi: 10.3897/phytokeys.75.9198 http://phytokeys.pensoft.net





Taxonomic and floristic novelties for Echeveria (Crassulaceae) in Central Michoacan, Mexico

Ignacio García-Ruiz¹, Dagoberto Valentín-Martínez², Pablo Carrillo-Reyes³,
Mihai Costea⁴

l Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Michoacán, Justo Sierra 28, Apdo. postal 109, C.P. 59510, Jiquilpan, Michoacán, México 2 Escuela de Biología de la Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México 3 Universidad de Guadalajara, Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, km. 15.5 carretera a Nogales, Predio Las Agujas, Zapopan, Jalisco 45110, México 4 Wilfrid Laurier University, Waterloo, Canada, 75 University Avenue West, Waterloo, Ontario, N2L3C5, Canada

Corresponding author: Mihai Costea (mcostea@wlu.ca)

Academic editor: Pavel Stoev | Received 12 May 2016 | Accepted 16 September 2016 | Published 25 November 2016

Citation: García-Ruiz I, Valentín-Martínez D, Carrillo-Reyes P, Costea M (2016) Taxonomic and floristic novelties for *Echeveria* (Crassulaceae) in Central Michoacan, Mexico. PhytoKeys 75: 1–12. doi: 10.3897/phytokeys.75.9198

Abstract

A new species, *Echeveria coruana*, is described and illustrated from the malpaís near San Andrés Corú, Michoacan, Mexico. The species belongs to series *Gibbiflorae* and the new taxon was compared with *E. purhepecha* and *E. patriotica*, with whom it shares the closest morphological affinities. Additionally, *E. yalmanantlaensis* an endangered species from Sierra of Manantlán Biosphere Reserve, State of Colima, was also discovered near San Andrés Corú and is reported for the first time from the State of Michoacan. The conservation status of both species was (re)evaluated according to the criteria of the International Union for Conservation of Nature.

Keywords

Conservation, Echeveria, malpaís, morphology, ser. Gibbiflorae, ser. Valvatae, taxonomy

Introduction

Echeveria DC. comprises ca. 140 species of which the majority (95%) have evolved in Mexico where the genus is characterized by a high degree of endemism (Uhl 1992, Thiede 1995, Meyrán and López-Chavez 2003, Pérez-Calix and Franco 2004, Vázquez et al. 2013). Among the infrageneric groups of this genus, ser. Gibbiflorae (Baker) Berger (sensu Walther 1972) is the third most diverse, being surpassed only by ser. Racemosae and ser. Nudae (Pilbeam 2008). It is noteworthy mentioning that the majority of new Echeveria species discovered in the last decade belong to ser. Gibbiflorae (García and Pérez-Calix 2007, Jimeno-Sevilla and Carrillo-Reyes 2010, Reyes and González 2010, Reyes et al. 2011a, 2011b, García and Costea 2014, Nieves-Hernández et al. 2014, Jimeno-Sevilla et al. 2015), which suggests an incomplete knowledge of the species diversity in this group.

The village of San Andrés Corú is located at ca. 12 km NE of the National Park Barranca del Cupatitzio, on the eastern side of the city of Uruapan, in the State of Michoacan (19°27.982'N, 101°56.644'W). This area is a part of the Trans-Mexican Volcanic Belt and has a particularly rich flora and vegetation consisting of a mixture of pine-oak and tropical deciduous forest elements (Rzedowski 1978). During the last years, systematic botanical explorations have been conducted to produce a floristic inventory of the malpaís surrounding San Andrés Corú. The malpaís ("badlands") is a landform that consists of relict yet recognizable lava fields that exhibit various degrees of erosion and vegetation succession stages depending on their age (Neuendorf et al. 2005). In some of the field trips undertaken NW and W-SW of the village, an unknown *Echeveria* belonging to ser. Gibbiflorae was discovered. Also, growing in the same type of ecosystem, at ca. 6 km SE of San Andrés Corú, E. yalmanantlanensis A. Vázquez & Cházaro, an endangered species of ser. Valvatae Moran previously known only from one population in the State of Colima (Vázquez et al. 2013), was also discovered. Thus, the first objective of this article is to describe the new species, which we named *E. coruana*, and to explore its morphological affinities with other species of ser. Gibbiflorae. The second aim is to report *E. yalmanantlanensis* as a new species for Michoacan.

Materials and methods

In addition to herbarium specimens, flowers and leaves of *E. coruana* and *E. yalmanantlanensis* were fixed in FAA (Ruzin 1999) for morphological studies. Several living plants of both species were collected with soil and cultivated in Jiquilpan, Michoacán for further study. We examined the basic morphology of both fresh and fixed flowers under a Nikon SMZ1500 stereomicroscope equipped with a PaxCam Arc digital camera and Pax-it 7.8 software (MIS Inc., Villa Park, Illinois). For scanning electron microscopy (SEM), we used hexamethydisilazane (HMDS) as an alternative for critical dry point (Wright et al. 2011). Fixed flowers were dehydrated using a series of ethanol steps (70%, 80%, 95% and 100%; each step 10 minutes), immersed for 10 minutes

in 1:1 ethanol: HMDS, and passed through three changes, each of 30 minutes in 100% HMDS. Samples were air dried and coated with 20 nm gold using an Emitech K 550 sputter coater. Micromorphological examination, measurements and pictures were taken at 10 kV using a Hitachi SU1510 variable pressure scanning electron microscope. Because only *E. coruana* is described, micromorphological data for pollen and seeds are presented only for this species. Additional images than those provided in the article have been uploaded in Phytoimages (Nickrent et al. 2006 onwards).

Results

The new species, E. coruana belongs to ser. Gibbiflorae, which as summarized by Kimnach (2003), includes glabrous plants, acaulescent or with monopodial stems; leaves are medium-sized to large, commonly narrowed basally into a pseudo-petiole; inflorescences are paniculiform; bracts are similar to the leaves but smaller; pedicels may reach 10 mm in length; calyx has unequal sepals; corolla is large, up to ca. 13 mm long, pentagonal-conical in bud, cylindrical-urceolate to campanulate at anthesis, ± glaucous, often with carinate petals exhibiting a basal cavity on the inner side; nectaries are large, fleshy; styles whitish to dark-red or nearly black. Echeveria coruana possesses a distinctive characteristic encountered only in four other species of ser. Gibbiflorae — E. dactylifera E. Walther (Walter 1972), E. novogaliciana J. Reyes, Brachet & O. González (Reyes et al. 2011), E. marianae I. García & Costea (García and Costea 2014), and E. rulfiana Jimeno-Sevilla, Santana Mich. & P. Carrillo (Jimeno-Sevilla et al. 2015): the presence of corolla appendages at the base of antipetalous staminal filaments. However, it markedly differs from these species in having smaller leaf rosettes, a different leaf morphology, shorter inflorescences, cincini with fewer flowers, and shorter pedicels. Among all these species, E. coruana has the shortest and most inconspicuous appendages. A detailed comparison of E. dactylifera, E. novogaliciana and E. marianae was provided by García and Costea (2014), and E. coruana can be easily contrasted with these species using the data included in Table 1. The most recently described species with corolla appendages, E. rulfiana, differs from E. coruana in its evidently caulescent habit and canaliculated leaves (Jimeno-Sevilla et al. 2015). Here we compared E. coruana with two other species, E. patriotica I. García & Pérez-Calix and E. purhepecha I. García, which appear morphologically closer even if they do not possess corolla appendages (Table 1).

Echeveria coruana I.García, D.Valentín & Costea, sp. nov.

urn:lsid:ipni.org:names:77158795-1

Figures 1, 2

Diagnosis. *Echeveria coruana* morphologically resembles most *E. patriotica* and *E. purhepecha*, with which it shares a similar flower morphology, but differs from both in having acaulescent or inconspicuous stems, acuminate leaves, and corolla appendages at the base

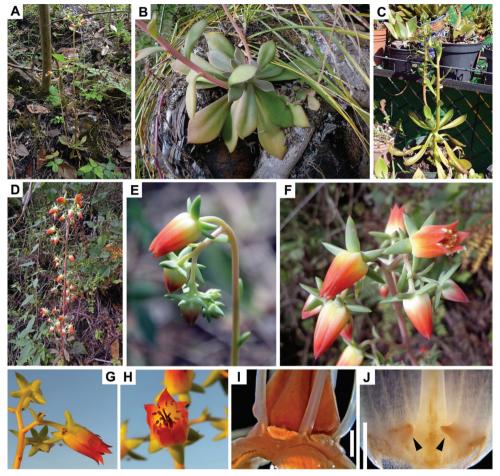


Figure 1. Habitat and general morphology of *Echeveria coruana*. **A** Habitat **B** Leaf rosette of type specimen **C** Developing plant (in cultivation) **D–F** Inflorescence **D** General view **E** Developing cincinus **F** Terminal cincinni **G–H** Flowers of type specimen viewed in the field from different angles **I–J** Flowers from type specimen fixed in FAA **I** Dissected flower (removed corolla) to show stamen bases and nectaries. **J** Conical appendages at the base of antipetalous staminal filaments (indicated with black arrows). Scale bars 1 mm.

of antipetalous stamen filaments. It differs from *E. patriotica* in having smaller leaf rosettes, 10–15 cm in diameter, smaller inflorescences, 28–65 cm long, longer pedicels, (1.3) 1.6–2.2 mm and a narrower corolla, 7–9 mm in diameter. It can be distinguished from *E. purhepecha* by the larger rosettes with spreading linear-oblanceolate to spathulate leaves, 8–16 cm long, and the larger corolla, 15–20 mm long, light-yellow to orange in the median part and orange-reddish at the tips of corolla lobes.

Type. MÉXICO. Michoacán: Municipio de Ziracuaretiro, lado noroeste de San Andrés Corú; 19°28.116′N, 101°57.410′W; 1730 m; bosque de encino-pino alterado con huertas de aguacate; 27 Nov 2015; *I. García & M. García 9138* (holotype: CIMI!, isotypes: DAO!, ENCB!, IEB!, MEXU!, MICH!, WLU!).

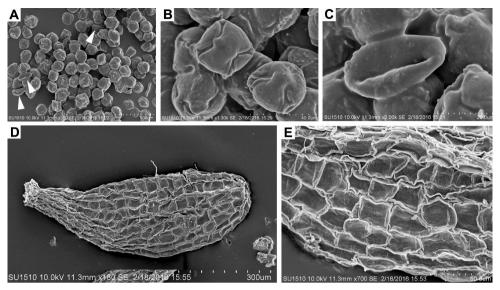


Figure 2. Scanning electron microscopy of *E. coruana*, pollen and seed (*García & García 9138*). **A–C** Heteromorphic pollen grains; arrows indicate a few 3-colpate, prolate pollen grains **B** 4-colpate (left, upper) and 3-colpate pollen (right, down) grains **C** 3-colpate, prolate pollen grain **D–E** Seed morphology.

Description. Perennial herb, glabrous, acaulescent or with an inconspicuous caudex, 3-8 cm long and 1-1.3 cm in diameter; rosette lax, 10-15 cm in diameter with 15–18 leaves; leaves fleshy, light-green to dark green in the median part and apex, leaf blade linear oblanceolate to spathulate, $8-16 \times 2-2.5$ cm, 0.5-1 cm thick at the base, margin entire, occasionally with a thin, red-colored line, apex acuminate, short mucronate, base narrowed to form a pseudo-petiole, 2-3 cm long, corrugated ventrally; inflorescence paniculiform thyrse, 1-3 per rosette, 28-65 cm long and 0.3-0.5 cm wide at the base, with 1–4 secondary axes (cincinni), each with 1–4(5) flowers; bracts spiralled, adpressed, green to yellowish-red, oblanceolate to oblong-lanceolate, 0.8–7.2 × 0.6–3 cm, 1.2–1.5 mm thick in the median part and 7–8.5 mm at the base, base auriculate, soon caducous; pedicels (1.3-) 1.6-2.2 mm long and 2-3 mm thick; calyx gamosepalous, star-shaped, the tube 1-1.5 mm long, lobes green, unequal, 6-9 × 3-4 mm, spreading to somewhat reflexed at anthesis, triangular-lanceolate; corolla pentagonalconical in bud, cylindrical-urceolate at anthesis, petals 15-21 × 4-6.5 mm, fused for 1-1.5 mm at the base, lanceolate, carenate, tips mucronate, erect to slightly deflexed, color whitish-yellow at the base, light-yellow to orange in the median part and orangereddish at the tips; nectaries reniform, 1.8-2.2 × 0.8-1 mm, white-yellowish; stamens 10, 5 antipetalous, 9-16 mm long (including the anthers), with a pair of conical or dome-like appendages at the base, 0.2-0.3 mm long; episepalous stamens 5, 10-16 mm long (including anthers); pollen polymorphic, most abundant type is 3-colpate, oblate to oblate-spheroidal in equatorial view and triangular or round in polar view, $30-34 \times 17-20$ mm, less common grains are 3-colpate, prolate, $34-38 \times 18-20$ mm

Table 1. Comparative morphology of *Echeveria coruana* with *E. patriotica* (García and Pérez-Calix 2007) and *E. purhepecha* (García 2011); "—" indicates data not available for comparison.

Character	Echeveria coruana sp. nov.	E. patriotica	E. purhepecha
Caudex	Acaulescent or inconspicuous	Evident	Evident
Length × diameter (cm)	3-8 ×1-1.3	20 × 1-2.5	8–11× 1.2
Rosette			
Diameter (cm)	10–15	10–35	8–10
Position of leaves in	S 1:	S 1:	Ascendant
rosette	Spreading	Spreading	Ascendant
Leaves			
Color	Light-green to dark green in the median part and apex	Green to reddish in the older leaves	Dark-green
Shape	Linear-oblanceolate to spathulate; apex acuminate, short mucronate	Oblong-obovate to spathulate; apex rounded, short mucronate	Oblong obovate; apex rounded, mucronate
Length (cm)	8–16	6–18	2–6.5
Width (cm)	2–2.5	3.5–11	1–2.5
Inflorescence			
Number of main axes	1–4	1–7	2–3
Length (cm)	28–65	20–100	15–30
Diameter at the base (cm)	0.3–0.5	1	0.3-0.6
Number of flowers/ cincinus	1–4(5)	1–8	1–7
Bracts			•
Shape	Oblong-lanceolate	Oblong-lanceolate	Oblong-obovate
Length (cm)	0.8–7.2	1.1–12	0.8–3
Width (cm)	0.6–3	0.6–4	0.3-1.3
Pedicel			
Length (cm)	(1.3) 1.6–2.2	0.7–1	0.3-1.3
Corolla shape at anthesis	Cylindrical-urceolate	Cylindrical-urceolate	Cylindrical-urceolate to campanulate
Length (mm)	15–20	18–20	10–12
Width (mm)	7–9	10–14	ca. 8
Sepals (calyx)	Spreading to ± reflexed at anthesis	Spreading at anthesis	Addressed at anthesis
Shape	Triangular-lanceolate	Triangular-lanceolate	Oblong-elliptic to lanceolate
Length x width (mm)	6–9 × 3–4	9–14 × 3-6	4-9 × 2.5-3.5
Petals			
Shape	Lanceolate	Lanceolate	Oblong-lanceolate
Length × width (mm)	15–21 × 4–6.5	18–20 × 5-7.5	10-11 × 4
(External) color	Whitish-yellow at the base, light- yellow to orange in the median part and orange-reddish at the tips	White to cream white at the base, orange-reddish in the median part and scarlet-red at the tips	Scarlet-red or coral from the base to the tip
Appendages	(1)2 per antipetalous staminal filament; conical or dome-like, 0.2–0.3 mm long	Absent	Absent
Nectaries			
Length × width (mm)	1.8-2.2 × 0.8-1	3 × 1	1.2 × 0.5
Color	White-yellowish	Purple-red	Pale yellow
Follicles	5–6 mm long, erect to somewhat spreading	12–18 mm long, erect	ca. 5 mm long, erect
Flowering	Nov-Jan	Oct–Jan	Sep-Nov
Geographical distribution	Michoacan, Mpio. Ziracuaretiro: Malpaís de San Andrés Corú	Jalisco, Mpio. Mazamitla	Michoacan, Mpio. Nuevo Parangaricutiro
Vegetation type	Mixture of oak-pine and tropical deciduous forest	Oak and oak-pine forest	Oak-pine forest

or 4-colpate, rectangular or spherical, $28-31 \times 17-20$ mm; in all pollen grains tectum is imperforate, scabrate; pollen grains eventually agglutinate into large masses; *ovary* with 5 apocarpous carpels, $9-11 \times 0.3-0.4$ mm; styles (including the stigmas) 4–5 mm long, red-purplish; *follicles* 5–6 mm long, erect to somewhat spreading; *seeds* numerous, oblong to obovate, light to dark-brown, reticulate, $0.5-0.65 \times 0.2-0.25$ mm; reticulum size 15-30 mm.

Discussion. A detailed comparison of *E. coruana* with *E. patriotica* and *E. pur*hepecha is presented in Table 1. If these three species are related from an evolutionary point of view, the corolla appendages have evolved at least two times in ser. Gibbiflorae. The antipetalous stamen appendages of E. coruana are considerably smaller and less complex than those of E. novogaliciana, E. marianae, E. dactylifera and E. rulfiana, the other species of ser. Gibbiflorae that are known to possess them (García and Costea 2014, Jimeno-Sevilla et al. 2015). García and Costea (2014) indicated that these appendages do not have a secretory function and their role may be to protect the nectar accumulated at the base of petals from pollinators lacking a specialized feeding apparatus. In E. coruana, the appendages are too small to cover the corolla cavities in which nectar accumulates. Alternatively, if E. coruana is evolutionarily related to these latter four species, the reduction of antipetalous corolla appendages in *E. coruana* likely indicates the loss of this hypothetical nectar defense function. Corolla appendages at the base of stamens have also evolved in Pachyphytum (Walther 1972, Thiede and Eggli 2007), a genus that forms a sister clade to the remaining "Echeveria group" (Carrillo-Reyes et al. 2009). A molecular study for ser. Gibbiflorae with more extensive sampling that of Carrillo and et al. (2009) is necessary to understand the evolutionary relationships among the numerous members of this group (Walther 1972), including the several recently described species.

Ecology. The new species grows in the understory of mixed pine-oak and tropical deciduous forest on volcanic basaltic rocky outcrops or small ledges. However, it has also been observed growing epiphytically on *Quercus* sp. The tree layer is dominated by *Quercus magnoliifolia* Née, *Ficus membranacea* C. Wright, *Juglans major* (Torr.) Heller, *Photinia microcarpa* Standl., *Bursera ariensis* (H.B.K.) Mc. Vaugh & Rzed., and *Clusia salvinii* Donn.; the most common shrubs are *Bursera bipinnata* (Sessé & Moc. ex DC.) Engl., *Montanoa bipinnatifida* (Kunth) C. Koch, *Montanoa frutescens* (Mairet) ex DC. and *Rhus terebinthifolia* Schltdl. & Cham. The herbaceous understory vegetation includes among others: *Arenaria lanuginosa* (Michx.) Rohrb, *Bonplandia geminiflora* Cav., *Tripogandra amplexicaulis* (Klotzsch ex C.B. Clarke) Woodson, *Phaseolus acutifolius* var. *latifolius* G.F. Freeman, and *Dryopteris maxonii* Underw. & C. Chr.

Phenology. November to January.

Etymology. The specific epithet derives from San Andrés Corú, the nearest village to the malpaís where the species was discovered. "Corú" in the local Purhépecha language means "a place where the quails sing".

Conservation status. *Echeveria coruana* is currently known only from three populations located at *ca.* 1–2 km from one another in the malpaís of San Andrés Corú. Although it is relatively common in the studied sites, it is threatened because of the

increasing demand and exploitation of volcanic rocks in the area. Furthermore, the recent establishment of avocado orchards at elevations of 1670–1750 m has led to significant habitat loss in the area, and this practice is likely to continue in the future. Although it was not possible to use GeoCAT (Bachman et al. 2011) to calculate the extent of occurrence because of the reduced number of localities from which the species is known, we determined the area of occupancy, which was 8 square km (based on 2 km cells). Therefore, using the IUCN (2012) criteria B2 biii, we preliminarily categorize this species as Critically Endangered (CR). More research in the field will be carried out in the future to determine the best strategy to mitigate the above mentioned threats.

Additional specimens examined. MÉXICO. Michoacán: Municipio de Ziracuaretiro, Malpaís de San Andrés Corú, bosque de encino-pino, 1676 m, 1 Dec 2012, *D. Valentín 502* (CIMI!, EBUM!); Malpaís de San Andrés Corú, lado oeste-suroeste de San Andrés Corú, 1660 m, 29 Apr 2015, *I. García*, *D. Valentín* and *A. Fuentes 9078* (CIMI!).

Echeveria yalmanantlanensis new for the flora of Michoacán

The exploration of the malpaís located at *ca.* 6 km SE of San Andrés Corú also led to an important floristic discovery: a new record of *E. yalmanantlanensis* (Fig. 3). This species has been considered in danger of extinction and endemic to the Cerro Grande Massif, which is situated in eastern Sierra of Manantlán Biosphere Reserve, Municipality of Comala, State of Colima, where it is known from one single population (Vázquez et al. 2013). More than a decade of concerted explorations conducted by multiple botanists to find additional populations at the type locality, the adjacent volcanic areas, Sierra de Manantlán Central, and Nevado de Colima, have been unsuccessful (reviewed by Vázquez et al. 2013). Under these circumstances, it was totally unexpected to discover it in Michoacan at about 210 km from the type locality. This finding suggests a disjunct distribution of *E. yalmanantlanensis*, which although rare may also be present at other localities in Central Michoacan.

Habitat and phenology of *E. yalmanantlanensis*. In Michoacan, *E. yalmanantlanensis* grows on volcanic rocks and occasionally as epiphyte in shady habitats that maintain sufficient humidity even during the dry season (Fig. 3). The vegetation at the new locality is very similar to that of *E. coruana* (see above), consisting of a mixture of pine-oak and tropical deciduous species. The vegetation at the type locality in Sierra of Manantlán includes some elements of tropical deciduous forest at 1500 m above the sea level; however, the companion species indicated by Vázquez-García et al. (2013)—*Jatropha bartlettii* Wilbur, *Bursera macvaughiana* Cuevas & Rzed., and *Agave attenuata* Salm-Dyck. — have not been observed at the new site in Michoacan. Furthermore, at the original site, oak-pine forest vegetation elements were absent. The substrate at the original site in Colima State is calcareous, while in Michoacan it is volcanic. Also the epiphytic habitat observed in Michoacan (Fig. 3) was not re-



Figure 3. *Echeveria yalmanantlensis* in the new habitat from Michoacan. **A** General habitat view of young epiphytic plants **B–D** Leaf rosettes and developing plants **E** Inflorescence.

ported from the type locality. The phenology is also somewhat different between the two sites: it extends to December at the new locality in Michoacan, while in Sierra of Manantlán plants were noted to flower from the end of July to the beginning of October. Only the climate is more or less similar at both sites, as it belongs to the type $(A)C(w)(i')(w_2)$ (García 1988), semi-warm, sub-humid, with an annual average temperature between 18° and 22°C and characteristics intermediate between warm and temperate climates.

Conservation status of *E. yalmanantlanensis*. Vázquez-García et al. (2013) proposed the inclusion of *E. yalmanantlanensis* in the Mexican Endangered Species Act as an endangered species (Norma Oficial Mexicana, NOM-ECOL-059-2010). In Michoacan, only three populations with very few mature individuals (4–10) were found. An evaluation of the conservation status based on the geographical distribution using GeoCAT (Bachman et al. 2011) revealed that the extent of occurrence and area of occupancy (based on 2 km cells) in Michoacan are 62.01 km² and 8 km², respectively. Including the population from Colima and using the IUCN (2012) criteria, we provisionally propose an endangered status (EN) for this species. Like in the case of *E. coruana*, the habitat of *E. yalmanantlanensis* is threatened by the development of avocado plantations and exploitation of volcanic rock.

Specimens examined. MEXICO. Colima: Municipio de Comala (originally cited as Jalisco-Colima because of the proximity to the border between the two states), camino a Campo Cuatro, Cerro Grande, on a rock of a limestone slope, 1550 m, 26 Sep 2011, *J. Antonio Vázquez-García, M. Cházaro B. & J. Padilla-Lepe 9175* (holotype: IBUG!; isotype: NY!). Municipios Comala border, camino de Campo Cuatro a La Añilera, Cerro Grande, tropical dry forest, on a rock of a limestone slope, 1500 m, 18 Jul 2004, *Vázquez-García & Contreras 7830a, 7830b* (IBUG!). Michoacán: Municipio de Ziracuaretiro, Malpaís de San Andrés Corú, Bosque de Encino, epífita sobre *Quercus* sp., 1513 m, 22 Dec 2012, *D. Valentín 537* (CIMI, EBUM!); Malpaís de San Andrés Corú, bosque mixto con encinos, sobre rocosidades, 1510 m, 29 Apr 2015, *I. García & D. Valentín 9077* (CIMI!); 15 Sep 2015, *I. García & D. Valentín 9077* (CIMI!, WLU!).

Acknowledgements

We would like to thank the managers/directors of the CIMI, EBUM and IEB herbaria for providing access to collections, and to David Jimeno Sevilla for reviewing the manuscript. We are also grateful to Jesús Contreras León for his help during the field trips, to Patricia Silva Sáenz for her constructive comments, and to Fidel Carrillo for providing the initial information about the location of *E. coruana*. Last but not least, the first author is grateful to COFAA and EDI, and in particular SIP projects 20141105 and 20150493 of the Instituto Politécnico Nacional, Mexico for supporting this research.

References

- Bachman S, Moat J, Hil AW, de la Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. ZooKeys 150: 117–126. doi: 10.3897/zookeys.150.2109
- Carrillo-Reyes P, Sosa V, Mort ME (2009) Molecular phylogeny of the Acre clade (Crassulaceae): Dealing with the lack of definitions for *Echeveria* and *Sedum*. Molecular Phylogenetics and Evolution 53: 267–276. doi: 10.1016/j.ympev.2009.05.022
- García E (1988) Modificaciones al sistema de clasificación climática de Koppen. Talleres Larios, S. A. 4th edición, México, 220 pp.
- García RI, Pérez-Calix E (2007) Una especie nueva de *Echeveria* (Crassulaceae) originaria del estado de Jalisco, México. Acta Botanica Mexicana 78: 125–132.
- García RI (2011) Nueva especie de *Echeveria* (Crassulaceae) del centro-occidente de Michoacán, México. Revista Mexicana de Biodiversidad 1: 63–67.
- García RI, Costea M (2014) *Echeveria marianae* (Crassulaceae), a new species from Jalisco, México. Phytotaxa 170(1): 35–040. doi: 10.11646/phytotaxa.170.1.4
- IUCN Standards and Petitions Subcommittee (2016) Guidelines for using the IUCN Red List categories and criteria. Version 12. http://www.iucnredlist.org/documents/RedListGuidelines.pdf [accessed 3.05.2016]

- Jimeno-Sevilla HD, Carrillo-Reyes P (2010) *Echeveria perezcalixii* (Crassulaceae), una especie nueva del occidente de México. Brittonia 62: 303–308. doi: 10.1007/s12228-010-9137-1
- Jimeno-Sevilla HD, Santana-Michel FJ, Carrillo-Reyes P (2015) Dos especies nuevas de Crassulaceae del Sur de Jalisco, México. Acta Botanica Mexicana 110: 71–88.
- Kimnach M (2003) *Echeveria*. In: Eggli U (Ed.) Illustrated handbook of succulent plants: Crassulaceae. Springer-Verlag, Berlin, 103–128.
- Meyrán J, López L (2003) Las Crasuláceas de México. Sociedad Mexicana de Cactología, A. C. México, D. F., 234 pp.
- Moran R (1974) Division of the genus *Echeveria* into series. In: Jacobsen H (Ed.) Lexicon of succulent plants. Blandford Press, London, 184–186.
- Nickrent DL, Costea M, Barcelona JF, Pelser PB, Nixon K (2006-onwards) *Phytoimages*. http://www.phytoimages.siu.edu [accessed 2 Septemeber 2016]
- Neuendorf KKE, Mehl JP Jr, Jackson JA (2005) Glossary of geology (5th ed). American Geological Institute, Alexandria, Virginia, 779 pp.
- Nieves-Hernández G, Vázquez-García JA, Muñiz-Castro MA, Cházaro-Basáñez M (2014) *Echeveria cerrograndensis* (Crassulaceae), a new species from Eastern calcareous Sierra de Manantlán, Colima, México. Phytotaxa 172: 247–255. doi: 10.11646/phytotaxa.172.3.5
- Norma Oficial Mexicana (NOM-059-ECOL2010) (2010) Protección ambiental. Especies nativas de México de flora y fauna silvestres. Categorías de riesgo y especificaciones para su inclusión, exclusion o cambio. Lista de especies en riesgo. Diario Oficial de la Federación, Instituto Nacional de Ecología, México, 78 pp.
- Pérez-Calix E (2008) Familia Crassulaceae. Flora de Bajío y de Regiones Adyacentes. Fasc. 156. Instituto de Ecología, A. C., Pátzcuaro, Michoacán,141 pp.
- Pérez-Calix E, Franco IS (2004) Crasuláceas. In: García-Mendoza AJ, Ordoñez MJ, Briones Salas M (Ed.) Biodiversidad de Oaxaca. Instituto de Biología, UNAM-Fondo Oaxaqueño para la Conservación de la Naturaleza-World Wildlife Fund, México, 209–217.
- Pilbeam, J (2008) The genus *Echeveria*. British Cactus and Succulent Society, Norwich, 333 pp. Rzedowski, J. 1978. *Vegetación de México*. Editorial Limusa, México, 432 pp.
- Reyes J, González O (2010) *Echeveria roseiflora* (Crassulaceae), una nueva especie para el estado de Jalisco, México. Cactáceas y Suculentas Mexicanas 55: 19–26.
- Reyes J, Brachet C, González O (2011a) *Echeveria guerrerensis* (Crassulaceae), una nueva especie para el estado de Guerrero, México. Cactáceas y Suculentas Mexicanas 56: 75–81.
- Reyes J, Brachet C, González O (2011b). *Echeveria novogaliciana*, una nueva especie de la familia Crassulaceae para los estados de Aguascalientes y Jalisco, México. Cactáceas y Suculentas Mexicanas 56: 82–95.
- Ruzin SE (1999) Plant microtechnique and microscopy. Oxford University Press, Oxford, 336 pp. Thiede J (1995) Quantitative phytogeography, species richness, and evolution of American Crassulaceae. In: Hart H, Eggli U (Eds) Evolution and systematics of the Crassulaceae, Backhuys, Leiden, 89–123.
- Thiede J, Eggli U (2007) Crassulaceae. In: Kubitzki K (Ed.) Flowering Plants. Eudicots, Vol. 9. Springer, Berlin, Heidelberg, 83–118. doi: 10.1007/978-3-540-32219-1_12
- Uhl CH (1992) Polyploidy, diploidy, and chromosome pairing in *Echeveria* (Crassulaceae) and its hybrids. American Journal of Botany 79: 556–566. doi: 10.2307/2444868

- Vázquez-García JA, Jimeno SD, Cuevas GR, Cházaro BM, Muñiz-Castro MA (2013) *Echeveria yalmanantlanensis* (Crassulaceae): A new species from Cerro Grande, Sierra de Manantlán, western Mexico. Brittonia 65: 273–279. doi: 10.1007/s12228-012-9274-9
- Vázquez-García JA, Nieves-Hernández G, Padilla-Lepe J, Nuño-Rubio AT, Cházaro-Basáñez M (2014) *Echeveria munizii* (Crassulaceae) a new species of epiphyte from tropical Volcán de Colima, Mexico. Phytotaxa 191:165–171. doi: 10.11646/phytotaxa.191.1.11
- Walther E (1972) Echeveria. California Academy of Sciences, San Francisco, 426 pp.
- Wright MA, Welsh M, Costea M (2011) Diversity and evolution of the gynoecium in *Cuscuta* (dodders, Convolvulaceae) in relation to their reproductive biology: two styles are better than one. Plant Systematics and Evolution 296: 51–76. doi: 10.1007%2Fs00606-011-0476-5