



<https://doi.org/10.11646/phytotaxa.629.3.2>

Spatial richness analysis and an evaluation of extinction risk for the genus *Pachyphytum* (Crassulaceae), with the description of a new species from Sierra Madre Occidental, Mexico

ARTURO CASTRO-CASTRO^{1,2,7,*}, JUAN PABLO ORTIZ-BRUNEL^{3,8}, HERIBERTO ÁVILA-GONZÁLEZ^{4,9}, ISAAC H. LICHTER-MARCK^{5,10}, PABLO CARRILLO-REYES^{3,11}, IRMA LORENA LÓPEZ-ENRÍQUEZ^{2,12} & MARCO ANTONIO BARVOSA-JIMÉNEZ^{6,13}

¹Consejo Nacional de Humanidades, Ciencias y Tecnologías, Av. Insurgentes Sur 1582, Col. Crédito Constructor, Alcaldía Benito Juárez, Ciudad de México, 03940, Mexico.

²Instituto Politécnico Nacional, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, CIIDIR – Durango, Sigma 119, Fracc. 20 de Noviembre II, Durango, Durango, 34234, Mexico.

³Universidad de Guadalajara, Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Camino Ing. Ramón Padilla Sánchez 2100, Las Agujas, Zapopan, Jalisco, 25510, Mexico.

⁴Jardín Etnobiológico Estatal de Durango, Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Durango (CIIDIR-Durango) – Consejo Nacional de Humanidades, Ciencias y Tecnologías, Blvd. Sahuatoba 204, Fracc. Parque Centenario, Durango, Durango, 34405, Mexico.

⁵Department of Botany, California Academy of the Sciences, 55 Music Concourse Dr, San Francisco, California 94118, USA.

⁶Consultora Forestal Durango S. de R.L. de C.V., Calle Doctores No 103 Col. 16 de Septiembre, Durango, Durango, 34030, Mexico.

⁷✉ art.castroc@hotmail.com; <https://orcid.org/0000-0002-2864-5180>

⁸✉ juanpbrunel@gmail.com; <https://orcid.org/0000-0002-0695-8143>

⁹✉ glezah@hotmail.com; <https://orcid.org/0000-0003-4110-8846>

¹⁰✉ ilichtermarck@berkeley.edu; <https://orcid.org/0000-0003-3575-6003>

¹¹✉ pablo.creyes@academicos.udg.mx; <https://orcid.org/0000-0001-9278-0208>

¹²✉ lorena_lopez05@yahoo.com.mx; <https://orcid.org/0000-0003-0075-5692>

¹³✉ cfago9319@gmail.com; <https://orcid.org/0000-0002-8818-6051>

*Corresponding author

Abstract

Pachyphytum is a genus of rupicolous succulents endemic to central Mexico. Here, we present a comprehensive list of currently recognized taxa in *Pachyphytum* with a review of biogeographical distribution data, a spatial richness analysis, and conservation assessments based on herbarium records and field work. *Pachyphytum* has been documented in 11 Mexican states, with the highest concentration of species (14) occurring in xerophilous scrubland, Chihuahuan Desert, and the Sierra Madre Oriental. All species of *Pachyphytum* are narrow endemics and were therefore categorized as at-risk of extinction according to IUCN criteria. Currently, taxa in *Pachyphytum* do not have formal protected status due to lack of inclusion on Mexico's list of endangered species. During fieldwork in preparation for this research, an undescribed *Pachyphytum* was encountered in Durango state, which we here describe as a new species based on a detailed morphological comparative study.

Key words: conservation, Madrense Ecoregion, Mexican Transition Zone, rupicolous plants, Southern Tepehuans

Introduction

Pachyphytum Link, Klotzsch & Otto in Klotzsch (1841: 9) is a monophyletic genus in the Crassulaceae family endemic to Mexico (Carrillo-Reyes *et al.* 2009, Vázquez-Cotero *et al.* 2017, de la Cruz *et al.* 2019). The genus comprises 24 species of rupicolous, suffrutescent perennial herbs, with a pendant or erect habit, and glabrous or viscid foliage (Kimmach 2010, Vázquez-Cotero *et al.* 2017, Pérez-Calix & Torres-Colín 2018, Meyrán 2019, Reyes-Santiago *et al.* 2019, 2020). Leaves in *Pachyphytum* may form a lax rosette or cluster toward the stem apex. Leaf blades are succulent, simple, flat or terete, green or purple, and sometimes conspicuously glaucous-farinoso. The inflorescence is an axillary scorpioid cyme or a cincinnus, with slightly imbricate succulent bracts. The flowers are gamosepalous and gamopetalous, with equal or unequal succulent sepals, these often longer or similar in size as the petals, these most frequently with two nectar-bearing appendages on the inner side, white, greenish or reddish, or with maculae at

the apex; stamens 10, 5 antepetalous with the filaments adnate to the corolla, and 5 antesepalous with free filaments; and 5 oblong nectaries placed at the base of the filaments (Thiede 2003, Thiede & Eggl 2007, Vázquez-Cotero *et al.* 2017). The set of morphological characters mentioned above, along with their relative rarity, makes *Pachyphytum* a group of plants highly valued in the ornamental plant trade. *Pachyphytum* have been traditionally subdivided into three sections based on morphological characters (Thiede 2003): *Dioctostemon* (Salm-Dyck 1854: 265) Walther (1931: 9), *Ixiocaulon* Moran (1968: 41), and *Pachyphytum* Moran (1968: 39). The most current taxonomic treatment by Thiede (2003) however, recognized only sections *Dioctostemon* and *Pachyphytum*. Recent floristic and taxonomic research has resulted in the description of several new species of *Pachyphytum* (Thiede 2003, Kimmach 2010, Pérez-Calix & Torres-Colín 2018, Reyes-Santiago *et al.* 2019, 2020), yet a comprehensive and up-to-date list of currently recognized taxa and their arrangement into sections has not been compiled.

Pachyphytum grow on rock outcrops and cliffs of various parent materials surrounded by a matrix of xerophytic scrub or oak forest, and are found in southern Tamaulipas, San Luis Potosí, Guanajuato, Querétaro, Hidalgo, and Michoacán, as well as western Mexico up to northern Jalisco and Zacatecas. Most *Pachyphytum* species have narrow geographic ranges, and many species are known only from their type localities and from a few nearby occurrences (Thiede 2003). Based on this pattern of allopatric, narrow endemism, we hypothesize that *Pachyphytum* species exhibit specialized climatic, edaphic, and topographical preferences. *Pachyphytum* therefore constitutes an ideal system to investigate the present and future risk of extinction on micro-endemic species.

Here, we compile an updated list of currently recognized species in *Pachyphytum*, arrange these into appropriate sections, and present a comprehensive review of biogeographical data, including distribution maps, spatial richness analyses and conservation assessments based on herbarium records and field work. *Pachyphytum* are found on difficult to access habitats found throughout a vast area, and we therefore expected that a comprehensive study of this genus would turn up taxonomic novelties. Indeed, during field work by the first author in 2019, a population of *Pachyphytum* was found in the state of Durango, a state in which the genus has never before been reported. Based on detailed morphological comparative study, we propose that these individuals constitute a new species of *Pachyphytum*, which we describe and illustrate here along with our review of distributional information for the genus as a whole.

Materials and methods

Sampling:—We sampled all species of *Pachyphytum* in the treatment of Thiede (2003), and in later taxonomic papers dealing with the genus (e.g. Pérez-Calix *et al.* 2008, Pérez-Calix & Torres-Colín 2018, Reyes-Santiago *et al.* 2019, 2020). *Pachyphytum cuicatecanum* (Reyes-Santiago *et al.* 2004: 80) Kimmach (2010: 125), was not included since phylogenetic evidence supports its recognition in the genus *Echeveria* de Candolle (1828: 401), despite showing morphological convergence with *Pachyphytum* (de la Cruz-López *et al.* 2019).

Geographic distribution data:—Taxonomic, geographic, ecological, and curatorial data were obtained from herbarium specimens in the following collections: CIIDIR, IBUG, IEB, MEXU, SLPM and UAS. We also compiled records from the IBUNAM database (IBUNAM 2022), the Red de Herbarios del Noreste de México (Sánchez-Escalante & Gilbert 2019) and the Southwest Environmental Information Network (SEINet; Gries *et al.* 2014). Taxonomic treatments and floristic studies were reviewed to generate a list of currently recognized taxa and to further inform geographic distributions. Anomalous records were flagged and inspected for misidentifications using digitized voucher specimens or detailed images provided by staff of the corresponding herbaria. When a specimen lacked geographic coordinates but possessed a detailed written description of the locality, we manually georeferenced it according to the strategy followed by Ortiz-Brunel *et al.* (2021). Occurrence data was cleaned by eliminating duplicate records and ambiguous locations, and then visualized using the program QGIS 3.4.8 (QGIS Development Team 2022). Finally, species richness was quantified by state (INEGI 2010), vegetation type (Rzedowski 1990), biogeographic province (Morrone *et al.* 2017), and by an arbitrary grid with a cell size of 0.5° in DIVA-GIS 4.2 (Hijmans *et al.* 2004).

Conservation status:—A risk category for each *Pachyphytum* taxon was determined based on field observations and our review of herbarium specimens according to the IUCN guidelines for categories and criteria (IUCN Standards and Petitions Committee 2022). We used GeoCAT (Bachman *et al.* 2011) to estimate the extent of occurrence (EOO) and area of occupancy (AOO) indices of each taxon that had at least three records. The AOO was estimated with the standard cell size of 2 km suggested by the IUCN. When a taxon's EOO was smaller than its AOO, we equalized both areas to be consistent with the assumption that AOO is contained within the EOO. Species with less than three records were evaluated based on their AOO only.

Morphological data:—Qualitative observations and quantitative measurements of morphological characteristics included in our species description (Simpson 2006) were based on vegetative and reproductive material viewed under a Zeiss Stemi 305 stereomicroscope (Zeiss, Jena, Germany). A revision of herbarium specimens as well as descriptions from the taxonomic literature were used to produce a diagnosis and a table comparing the new species to the currently recognized taxa of *Pachyphytum*.

Results

Biogeographical data and extinction risk categories for *Pachyphytum*

Distribution and richness:—The diversity and distribution of *Pachyphytum* within the major political units of Mexico, vegetation types, and biogeographic provinces is presented in Table 1. *Pachyphytum* has been documented in 11 Mexican states (Figure 1). The states with highest species richness were Guanajuato with seven species and Querétaro with six species. Hidalgo and San Luis Potosí states both contain four species. Fourteen *Pachyphytum* species occur in areas of xerophilous scrubland and 13 occur in areas of conifer and oak forest. Eight species were found within tropical deciduous forests, and one was recorded in grasslands. The Chihuahuan Desert (CHIH) and the Sierra Madre Oriental (SMOr) hosted most of the diversity of *Pachyphytum* with 13 and 11 species recorded, respectively. Three species are distributed in the Sierra Madre Occidental (SMOc) and two in the Trans-Mexican Volcanic Belt (TVB) respectively.

In the species richness grid cell analysis, the cells with the highest number of species were found at the confluence of the southern CHIH and the SMOr (Figure 2). One cell that contained four species was found at the border of Querétaro and Hidalgo. Two cells with three species were in Querétaro, near its border with Guanajuato and San Luis Potosí, and another located entirely in Guanajuato. Cells containing two species of *Pachyphytum* were found in Aguascalientes, Hidalgo, Guanajuato, and San Luis Potosí.

Extinction risk categories:—All the species of *Pachyphytum* were categorized as being at various levels of at-risk of extinction (Table 1). Using AOO, 10 species of *Pachyphytum* qualify as critically endangered, while based on EOO estimates, 15 species qualify as critically endangered. Fourteen species should be designated as endangered if AOO estimates are used, while seven would be evaluated as such based solely on EOO. In some important cases, the AOO results differed from those of EOO (Table 1).

Morphological data analyses:—Field work uncovered a *Pachyphytum* population in southern Durango state in SMOc, where the genus has not been reported before. Based on detailed morphological comparative study, specifically the length of the stems (>30 cm long), leaves elliptic or obovate, fertile bracts >10 mm long and petals with a central abaxial red spot, individuals in the Durango population resemble *P. contrerasii* Pérez-Calix, García & Cházaro in Pérez-Calix *et al.* (2008: 64), *P. kimnachii* Moran (1967: 204), *P. viride* Walther (1937: 210) and *P. werdermannii* Poelln. in Fedde (1937: 2). Distinctive differences between these taxa and the Durango population are presented in Table 2.

The new populations differed from *P. contrerasii* in the development of shorter and a more compact cincinnus, larger calyx lobes and different in shape, and in the size, shape and color of the petals, filaments, and style. The new population and *P. contrerasii* do not overlap in their biogeographical ranges; furthermore, the former was found in *Pinus-Quercus* forest in the Sierra Madre Occidental and *P. contrerasii* in tropical deciduous forest in the Transmexican Volcanic Belt. Also, the new populations differed from *P. kimnachii* in having elliptic or obovate leaves, ovate peduncle bracts, 12–22 mm long, a shorter cincinnus with fewer flowers, small floral bracts, in the form, size and color of corolla lobes, and size and color of stamens. The new populations and *P. kimnachii* were separated by ~500 km and occurring in distinctive biogeographical provinces of Mexico. Likewise, the new populations differed from *P. viride* in having elliptic or obovate leaves, ovate and pale reddish to pinkish orange peduncle bracts, oblong longer calyx lobes, and white stamens. Moreover, the new populations grow in *Pinus-Quercus* forest in the Sierra Madre Occidental, while *P. viride* in xerophytic scrub in the Sierra Madre Oriental. Finally, the new populations can also be differentiated from *P. werdermannii* by its ovate peduncle bracts, pale green and slightly pruinose cincinnus, ovate floral bracts, white corolla lobes with a ventral broad bright red spot, longer antipetalous stamens and white filaments. The new populations and *P. werdermannii* also differed in their ecological preferences and geographical distribution (Table 2, Figure 1).

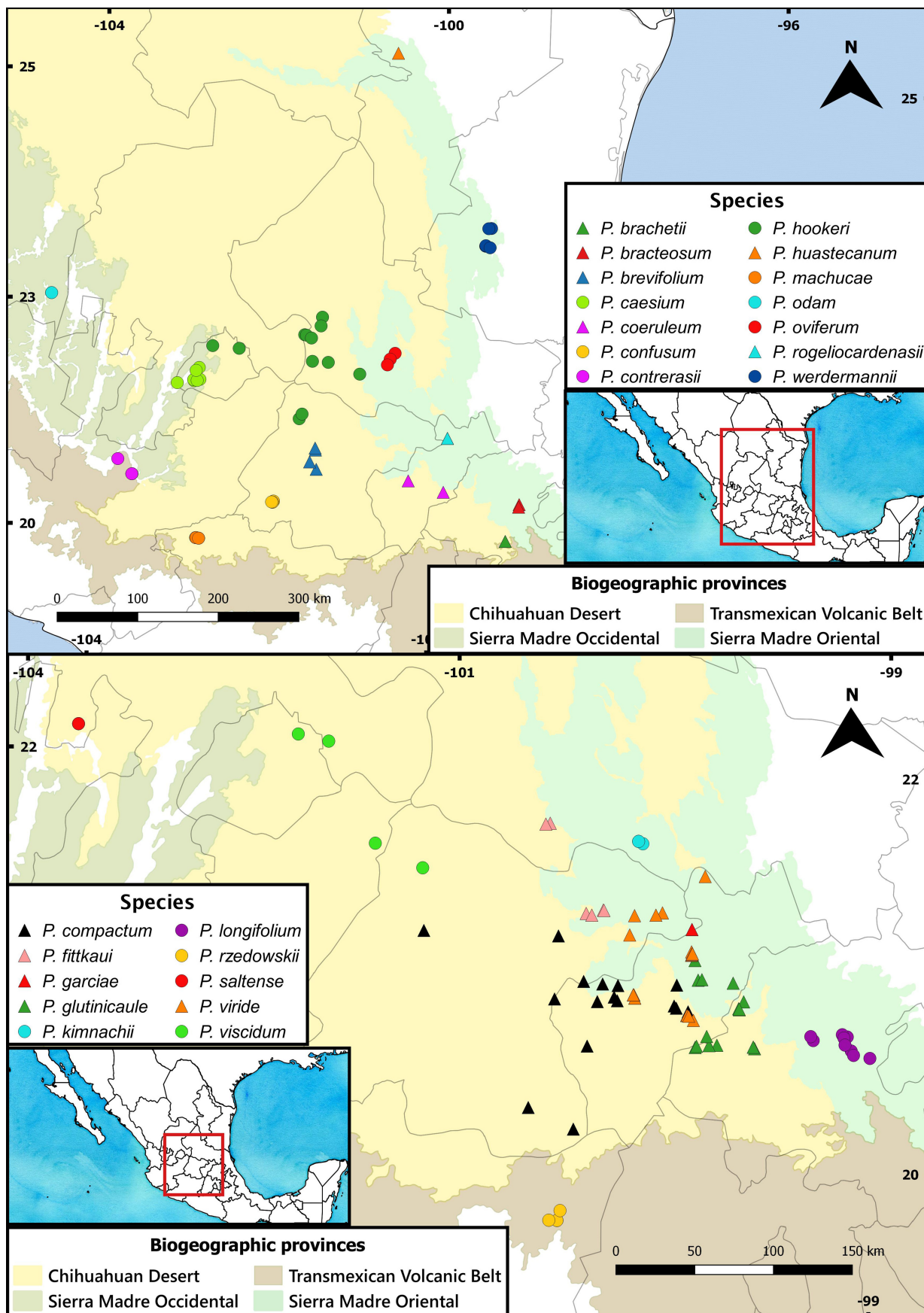


FIGURE 1. Diversity and distribution of the genus *Pachyphytum* in Mexico. Biogeographic provinces according to Morrone *et al.* (2017).

TABLE 1. Taxonomic diversity, distribution, and extinction risk of the genus *Pachyphytum*, with all currently recognized species assigned to infrageneric taxa. State names are abbreviated as follows: Aguascalientes (AGS), Guanajuato (GTO), Durango (DGO), Hidalgo (HGO), Jalisco (JAL), Michoacán (MICH), Nuevo León (NL), Querétaro (QRO), San Luis Potosí (SLP), Tamaulipas (TAMPS), and Zacatecas (ZAC). Vegetation types follow designations in Rzedowski (1990): Conifer-Oak Forest (COF), Grassland (GRASS), Tropical Deciduous Forest (TDF), Xerophilous Scrubland (XS). Biogeographic provinces follow Morrone *et al.* (2017): Chihuahuan Desert (CHIH), Sierra Madre Occidental (SMOc), Sierra Madre Oriental (SMOr), Trans-Mexican Volcanic Belt (TVB). Extinction risk categories follow the IUCN (2022): Critically Endangered (CR), Endangered (EN), and Vulnerable (VU). AOO: area of occupancy, EOO: extent of occurrence.

Species	Records	State	Vegetation type	Biogeographical province	AOO (km ²)	EOO (km ²)	Risk category (AOO/EOO)
<i>Pachyphytum</i> section <i>Diotostemon</i>							
1. <i>P. brevifolium</i> Rose	4	GTO	COF, TDF	CHIH	16	102.9	EN/EN
2. <i>P. coeruleum</i> J.Meyrán	2	QRO	XS	CHIH	8	-	CR
3. <i>P. compactum</i> Rose	18	GTO, QRO	COF, XS	CHIH, SMOr	68	11281	EN/VU
4. <i>P. hookeri</i> (Salm.-Dick) A.Berger	12	AGS, GTO, SLP	COF, XS	CHIH, SMOc	48	11624.9	EN/VU
5. <i>P. huastecanum</i> J.Reyes, Etter & Kristen	1	NL	XS	SMOr	4	-	CR
6. <i>P. viscidum</i> J. Reyes & de la Cruz-López	4	AGS, GTO, JAL, ZAC	GRASS, XS	CHIH	16	1236.3	EN/EN
<i>Pachyphytum</i> section <i>Ixiocaulon</i>							
7. <i>P. fitkaii</i> Moran	6	GTO, SLP	COF, XS	CHIH, SMOr	20	420.7	EN/EN
8. <i>P. glutinicaule</i> Moran	17	HGO, QRO	COF, XS	CHIH, SMOr	60	1449.1	EN/EN
<i>Pachyphytum</i> section <i>Pachyphytum</i>							
9. <i>P. brachetii</i> J.Reyes, O.González & A. Gut.	2	HGO	XS	CHIH	4	-	CR
10. <i>P. bracteosum</i> Klotzsch	2	HGO	XS	SMOr	8	-	CR
11. <i>P. caesium</i> Kinnach & Moran	7	AGS	COF, TDF	CHIH, SMOc	28	214	EN/EN
12. <i>P. confusum</i> Pérez-Calix, Guadián-Marín & I. García	5	GTO	TDF	CHIH	8	8	CR/CR
13. <i>P. contrerasii</i> Pérez-Calix, I. García & Cházaro	5	JAL	TDF	TVB	8	8	CR/CR
14. <i>P. garciae</i> Pérez-Calix & Glass	2	QRO	COF	SMOr	8	-	CR
15. <i>P. kinnachii</i> Moran	3	SLP	XS	SMOr	12	12	EN/CR
16. <i>P. longifolium</i> Rose	9	HGO	XS	SMOr	36	224.7	EN/EN
17. <i>P. machucae</i> I.García, Glass & Cházaro	7	MICH	TDF	CHIH	8	8	CR/CR
18. <i>P. odam</i> Art.Castro & P. Carrillo, <i>sp. nov.</i> here described	2	DGO	COF	SMOc	8	-	CR
19. <i>P. oviferum</i> Purpus	3	SLP	XS	CHIH, SMOr	12	12	EN/CR
20. <i>P. rogeliocardenasii</i> Pérez-Calix & R.Torres	3	QRO	COF, TDF	SMOr	12	12	EN/CR
21. <i>P. rzedowskii</i> I.García, Pérez-Calix & J.Meyrán	4	MICH	COF, TDF	TVB	12	16.1	EN/CR
22. <i>P. saltense</i> Brachet, J. Reyes & Mondragón	3	ZAC	COF	CHIH	4	-	CR
23. <i>P. viride</i> E.Walther	19	GTO, QRO	COF, XS	CHIH, SMOr	48	2898.1	EN/EN
24. <i>P. werdermannii</i> Poelln.	7	TAMPS	COF, XS	SMOr	16	97.8	EN/CR

TABLE 2. Comparison of morphological, phenological and geographical traits between *Pachytum sp. nov.* and related species.

Character	<i>P. contrerasii</i>	<i>P. kinnachii</i>	<i>P. sp. nov.</i>	<i>P. viride</i>	<i>P. werdermannii</i>
Leaves (shape, length, width, thickness, color)	elliptic to oblanceolate; 4–7.5 × 1.5–2.5 cm; 5–7 mm thick; green to pinkish at base, lavender-grey to bluish green at apex, pruinose	elliptic-oblong, oblanceolate or subrhombic; 5–10 × 1.8–3.5 cm; 9–10 mm thick; pale purplish, pruinose	elliptic or obovate; (4.5–)6–10.5 × (1.5–)2–3.5 cm; 6.5–10 mm thick; pale green to pale reddish to pinkish orange, slightly pruinose	subcylindrical to semiterete; 6–14 × 1.5–3 cm; 11–17 mm thick; yellowish-oil green, to calla-green beneath, slightly pruinose	elliptic to oblong; 4–10 × 1.5–3.5 cm; 5–12 mm thick; green to pale reddish, pruinose
Peduncle (length)	20–25 cm	15–25 cm	15–26 cm	10–35 cm	15–25 cm
Peduncle bracts (shape, length, width, color)	oblong; 8–16 mm × 3–8 mm; pale reddish to pinkish orange	ovate to elliptic or subrhombic; 10–30 mm × 5–10 mm; pale purplish	ovate; 12–22 mm × 5–12 mm; pale reddish to pinkish orange	elliptic to subrhombic; 15–35 × 4–14 mm; greenish white	elliptic to lanceolate or sometimes linear; 15–27 × 3–12 mm; pale green to almost white
Cincinnus (length, flowers number, color)	10–16 cm long; 12–24 flowers; green to olive and pink at the base, pruinose	6–23 cm long; 12–28 flowers; pale green, slightly pruinose	8–9 cm long; 15–18 flowers; pale green to pink, slightly pruinose	5–12 cm long; 10–22 flowers; greenish white, glaucous	5–11 cm long; 10–22 flowers; greenish white, glaucous
Floral bracts (shape, length, width)	oblong-ovate; 6–16 mm × 3–10 mm	ovate; 18–25 × 8–12 mm	ovate; 10–20 × 5–14 mm	ovate, obovate, or rhombic; 15–30 × 7–18 mm	ovate to elliptic; 15–20 × 7–10 mm
Pedicel	2–4 mm × 2–3 mm	3–7 mm × 2–3.5 mm	3–7 mm × 2.5–4 mm	2–6(–8) × 1.5–3 mm	3–8(–15) × 1–2 mm
Largest calyx lobes	oblong-obovate; 9–12 × 3.5–7 mm	elliptic-oblong; 15–28 × 4–11 mm	oblong; 15–18 × 7–9 mm	elliptic-oblong to spatulate; 11–19 × 4–9 mm	oblong; 12–19 × 4.5–8 mm
Shortest calyx lobes (shape, length, width)	oblong; 6–9 × 3–4 mm	triangular-oblong; 9–15 × 2–4 mm	oblong; 10–13.5 × 3.2–5.5 mm	oblong; 10–17 × 3–6 mm	oblong-lanceolate; 10–16 × 2.5–4.5 mm
Corolla lobes (shape, size, color)	oblong; 7–8 mm × 3–3.5 mm; light green with a ventral crimson spot	triangular-lanceolate; 13–17 mm × 3.5–4.5 mm; white or light pink with a ventral crimson spot	oblong; 7.5–11 mm × 3.5–4.3 mm; white with a broad ventral bright red spot	oblong-oblanceolate; 8–14 × 2.5–6 mm; white with a ventral dark crimson spot	oblong; 9.5–12.5 × 3–4 mm; light pink with a dark ventral crimson spot
Stamens (length, color)	antipetalous 3–4 mm long; antisepalous 4–5 mm long; both yellow-cream or whitish below and scarlet above	antipetalous 5–8 mm long; antisepalous 7–10 mm long; both whitish below and carmine above	antipetalous 4–5 mm long; antisepalous 6–7 mm long; both white	antipetalous 2–3 mm long; antisepalous 4–8 mm; both yellowish below, red above	antipetalous 3–3.5 mm long; antisepalous 6–9 mm; both whitish below, red above
Style	4–5 mm long	7–9 mm long	7–8.5 mm long	4.5–8 mm long	5–7 mm long
Nectaries	elliptical; 1–1.2 mm wide; yellowish	elliptical; 1.9–2.6 mm wide; yellowish	elliptical; 2.2–2.5 mm wide; pale yellow	elliptical; 2–3 mm wide; yellowish	elliptical; 1.5–2 mm wide; yellowish
Habitat	Tropical deciduous forest	<i>Pinus-Quercus</i> forest	<i>Pinus-Quercus</i> forest	Xerophytic scrub	Xerophytic scrub
Distribution	Central Jalisco	South central San Luis Potosí	South Durango	North Guanajuato, north and central Querétaro	Southwest Tamaulipas
Elevation range	1450–1500 m	1750–1900 m	2080–2115 m	1000–2350 m	550–915 m
Biogeographic provinces	Trans-Mexican Volcanic Belt	Sierra Madre Oriental	Sierra Madre Occidental	Chihuahuan Desert, Sierra Madre Oriental	Sierra Madre Oriental

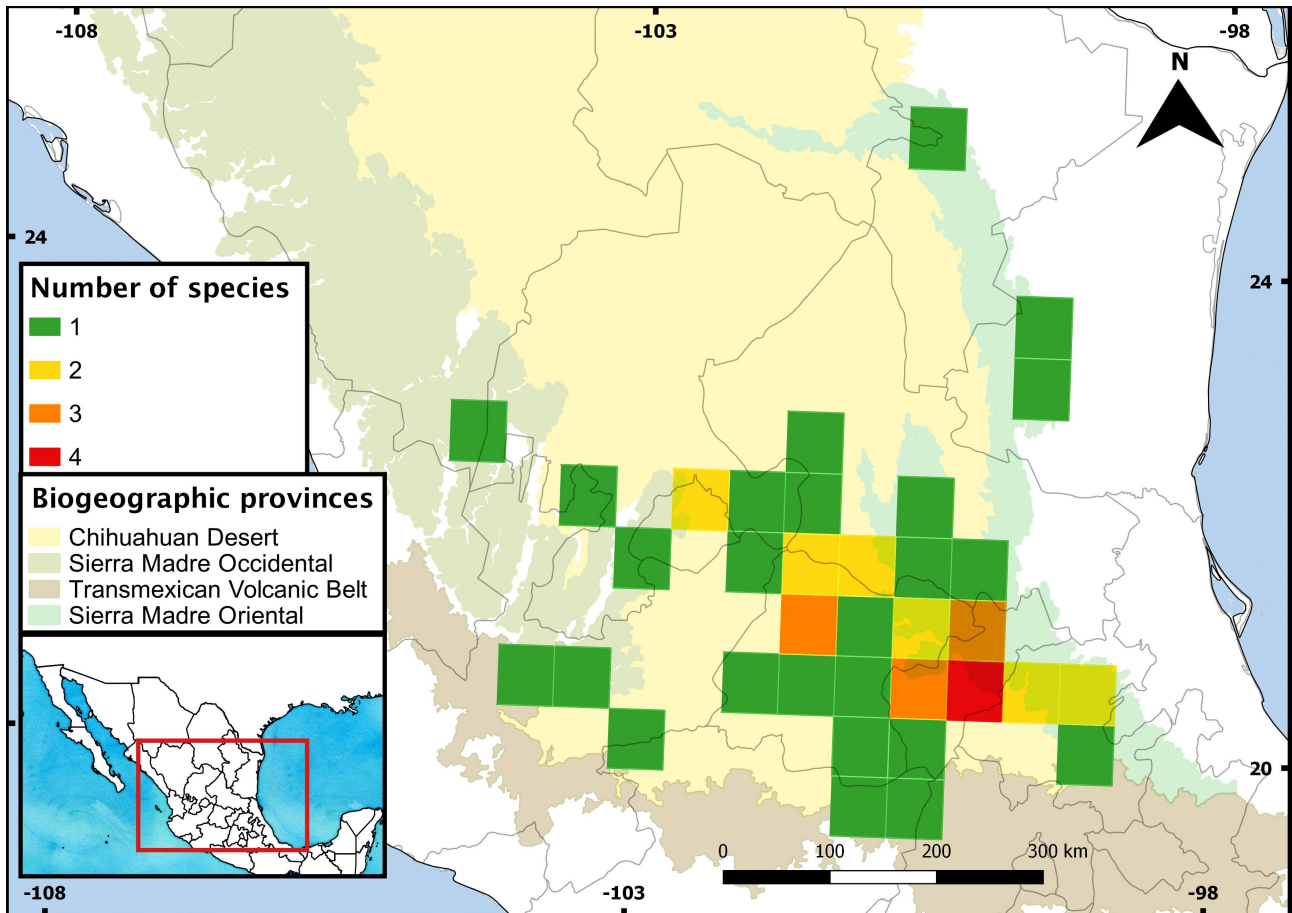


FIGURE 2. Species richness by grid cell of *Pachyphytum*. Biogeographic provinces according to Morrone *et al.* (2017).

Discussion

Biogeographical data and extinction risk categories:—*Pachyphytum* is a Mexican endemic genus distributed across the central portion of the country. Most of the species are micro-endemics with a very narrow range (Thiede 2003). The highest species richness of *Pachyphytum* occurs around the ecotone of the CHIH with the SMOr, mostly at the border between Guanajuato, Hidalgo, Querétaro and San Luis Potosí states. Many other micro-endemic species of Crassulaceae also occur in this area (Moran 1963; Pérez-Calix & Glass 1999; Pérez-Calix & Torres-Colin 2018), which is as an important center of endemism and a refugium for vascular plants (Sosa *et al.* 2020).

Pachyphytum species occur in xerophilous scrubland or its ecotone with temperate forests. This agrees with our biogeographic results showing that cells with the highest number of species were found at the confluence of the southern CHIH and the SMOr, in the borders between arid and temperate environments, and coincides with the San Luis Potosí and Hidalgo-Querétaro Mexican regional centers of species richness and endemism recognized by Thiede (1995).

Most *Pachyphytum* species are micro endemics, but despite being under pressure from harvesting as ornamental plants, particularly during Christmas festivities (Cabrera-Luna *et al.* 2007), none are included in Mexico's federal protected species list, the NOM-059-SEMARNAT-2010 (SEMARNAT 2019). Our results show that, based on AOO and EOO, all *Pachyphytum* species should be evaluated as being at-risk. As stated by the IUCN (2022), species with small AOO are typically habitat specialists. This is the case in most *Pachyphytum* species, which grow exclusively on vertical rock cliffs surrounded by xerophytic or temperate vegetation. Due to their inaccessibility, vertical rock habitats are difficult places in which to estimate the population size and distribution of rare plants. In such cases, we suggest that AOO may be a useful metric to evaluate appropriate risk categories (Keith 1998). *Pachyphytum* occur in understudied habitats, and therefore, it is feasible that these patterns are artifacts of a lack of sampling in inaccessible regions.

Taxonomic novelty:—The *Pachyphytum* populations located in Durango, where the genus has never before been reported, represents the northernmost range of the genus on the Pacific slope of Mexico. Based on the morphological analysis of the individuals in the population, we conclude that this is an undescribed species. Considering the leaf shape (broadest at or near the middle) and petal length ((8–)10–17 mm), we hypothesized that the new species may be closely related to the *P. werdermannii* informal group identified by Thiede (2003), and possibly composed by *P. contrerasii*, *P. fittkaui* Moran (1971: 26), *P. kimnachii*, *P. viride*, and *P. werdermannii*. These five species all possess stems >30 cm long, elliptic or obovate leaves, fertile bracts >10 mm long, and petals with an abaxial red spot in the middle.

Although *Pachyphytum* is clearly monophyletic, its infrageneric relationships have not been elucidated, and it has been pointed out that low phylogenetic resolution in this group may be due to convergence among characters and recent diversification (Thiede 2003, de la Cruz *et al.* 2019). Thus, based on morphology (Moran 1968), we conclude that the new species belongs in *Pachyphytum* section *Pachyphytum* due to the presence of imbricate cincinnus bracts, calyx exceeding the corolla, unequal calyx segments and white petals with a red spotted adaxial surface.

Taxonomic treatment

Pachyphytum odam Art. Castro & P. Carrillo, *sp. nov.*, Figure 3

Diagnosis:—*Pachyphytum odam* is morphologically similar to *P. contrerasii*, *P. kimnachii*, *P. viride* and *P. werdermannii* due to the length of the stems, the shape of the leaves, the size of the fertile bracts, and the petals with an abaxial red spot in the middle. From *P. contrerasii* and *P. viride*, it differs in possessing a shorter and more compact cincinnus, larger calyx lobes of a distinct shape, and the size, shape and color of the petals, filaments, and style. From *P. kimnachii* it differs principally in the shape, size and length of leaves, peduncle bracts, cincinnus, and stamens, and in the number of flowers. Finally, *P. odam* can be differentiated from *P. werdermannii* by the peduncle and floral bract shape, the color of the cincinnus and corolla lobes, and the length and color of antipetalous stamens.

Type:—MEXICO. Durango. Mezquital: Comunidad de Santa María de Ocotán y Xoconoxtle, Anexo La Muralla, elev. 2115 m, 14 March 2019 (fl, fr), *A. Castro-Castro et al.* 4442 (holotype CIIDIR!, isotypes IBUG!, MEXU!, SLPM!).

Description:—Suffrutescent herb, succulent, pendant, decumbent, glaucous, glabrous; stems often unbranched or branched from near the base, 30–60 cm long, 1.4–1.8 cm thick, adventitious fibrous roots and conspicuous leaf scars at the nodes. Leaves 12–26, sessile, arranged in a disordered spiral at the apex of the stem, in lax rosettes, laminas elliptic or obovate, (4.5–)6–10.5 × (1.5–)2–3.5 cm, 6.5–10 mm thick, elliptical-concave in cross section, conspicuous rib on dorsal surface, apex rounded, margin entire, succulent, pale green to pale reddish to pinkish orange, slightly pruinose, glabrous. Inflorescence axillary, near the apex of the branches; peduncle 15–26 × 0.4–0.6 cm, pale reddish to pinkish orange, pruinose; sterile bracts 2–3, deciduous, ovate, 12–22 mm × 5–12 mm, acute, obtuse-cuneate, flat, pale reddish to pinkish orange; cincinnus 8–9 cm long, 15–18 flowers, pale green, slightly pruinose; flower bracts imbricate, ovate, 10–20 × 5–14 mm, acute to slightly apiculate to mucronate, obtuse-oblique, green, yellowish green to pinkish orange with maturity. Flowers on a turbinate pedicel, 3–7 mm × 2.5–4 mm, green, pruinose. Calyx 5-lobate, lobes unequal, the largest oblong, 15–18 × 7–9 mm; the smaller oblong, 10–13.5 × 3.2–5.5 mm, both acute, mucronate, obtuse. Corolla 5-lobate, lobes oblong, 7.5–11 mm × 3.5–4.3 mm, apex acute, white with a broad ventral bright red spot in the middle; appendages obtuse, red. Stamens 10, flattened, 5 antipetalous, 4–5 mm long, 5 antisealous, 6–7 mm long, white with red apex; anthers 1.9–2.1 × 0.9–1 mm; pollen pale yellow. Nectaries transversely elliptical, 2.2–2.5 mm long, pale yellow. Ovary 6–6.5 mm long; style 7–8.5 mm long. Follicles 7.5–8 mm long. Seeds numerous, clavate to pyriform, 0.5–0.6 × 0.19–0.22 mm.

Distribution and habitat:—*Pachyphytum odam* grows on north facing cliffs bordering the wide and deep canyon of the river El Navío (Mezquital municipality, Durango), in which one of the only two known populations of *Pinus maximartinezii* Rzed. (1964: 17) also occurs (González-Elizondo *et al.* 2011). The area is dominated by *Pinus-Quercus* forest, where, in addition to *P. maximartinezii*, the following trees occur: *Arbutus madrensis* S. González, *A. tessellata* P.D. Sørensen, ex Klotzsch, *Fraxinus* sp., *Pinus lumholtzii* B.L. Rob. & Fernald, *Quercus chihuahuensis* Trel., *Q. gentryi* C.H. Mull., *Q. praeco* Trel., *Q. resinosa* Liebm. and *Yucca* sp. Associated shrubs include *Ageratina* spp., *Arctostaphylos pungens* Kunth, *Chiococca* sp., *Comarostaphylis polifolia* (Kunth) Zucc., *Lagascea helianthifolia* Kunth, *Montanoa* sp., *Opuntia* spp., *Rhus aromatica* Aiton, *Salvia melissodora* Lag., *Stevia* sp., and *Vernonia* sp. Other plant species that grow in association with *P. odam* on vertical rock outcrops are *Agave schidigera* Lem., *Dasyliirion*

sp., *Ferocactus histrix* (DC.) G.E. Linds., *Ficus petiolaris* Kunth, *Hechtia* sp., *Mammillaria* sp., *Muhlenbergia* sp., *Nolina* sp. and *Tillandsia* sp. (Figure 4). It occupies an elevational range from 2080 to 2115 m (Table 2).

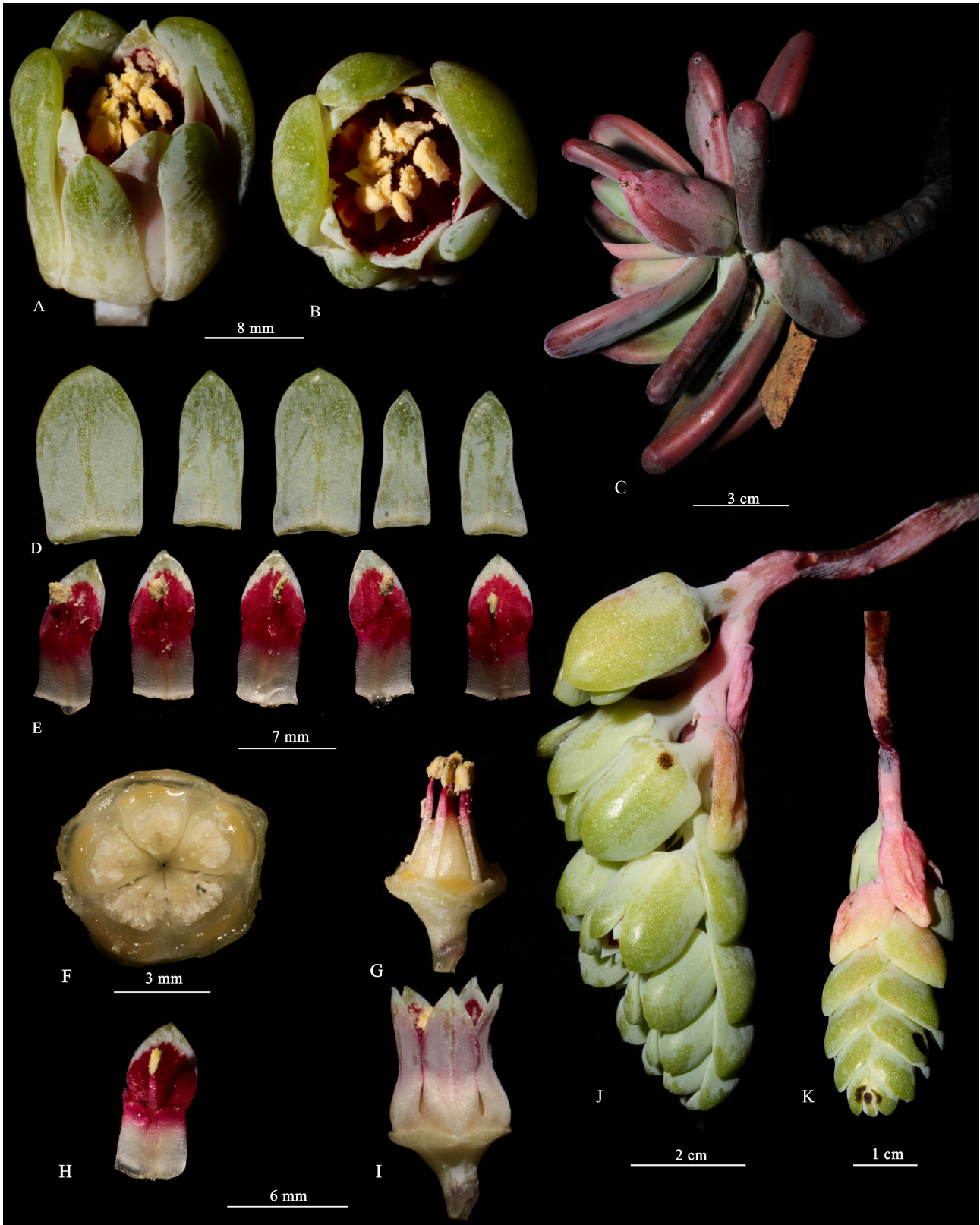


FIGURE 3. *Pachyphytum odam* Art. Castro & P. Carrillo. **A–B.** Lateral and front view of the flower. **C.** Lateral view of the rosette. **D.** Calyx lobes. **E.** Corolla lobes. **F.** Transverse view of the ovary. **G.** Lateral view of the androecium and gynoecium. **H.** Petal abaxial view. **I.** Lateral view of the corolla without the calyx. **J–K.** Lateral and adaxial view of the cincinnus. Photographs: Arturo Castro Castro.

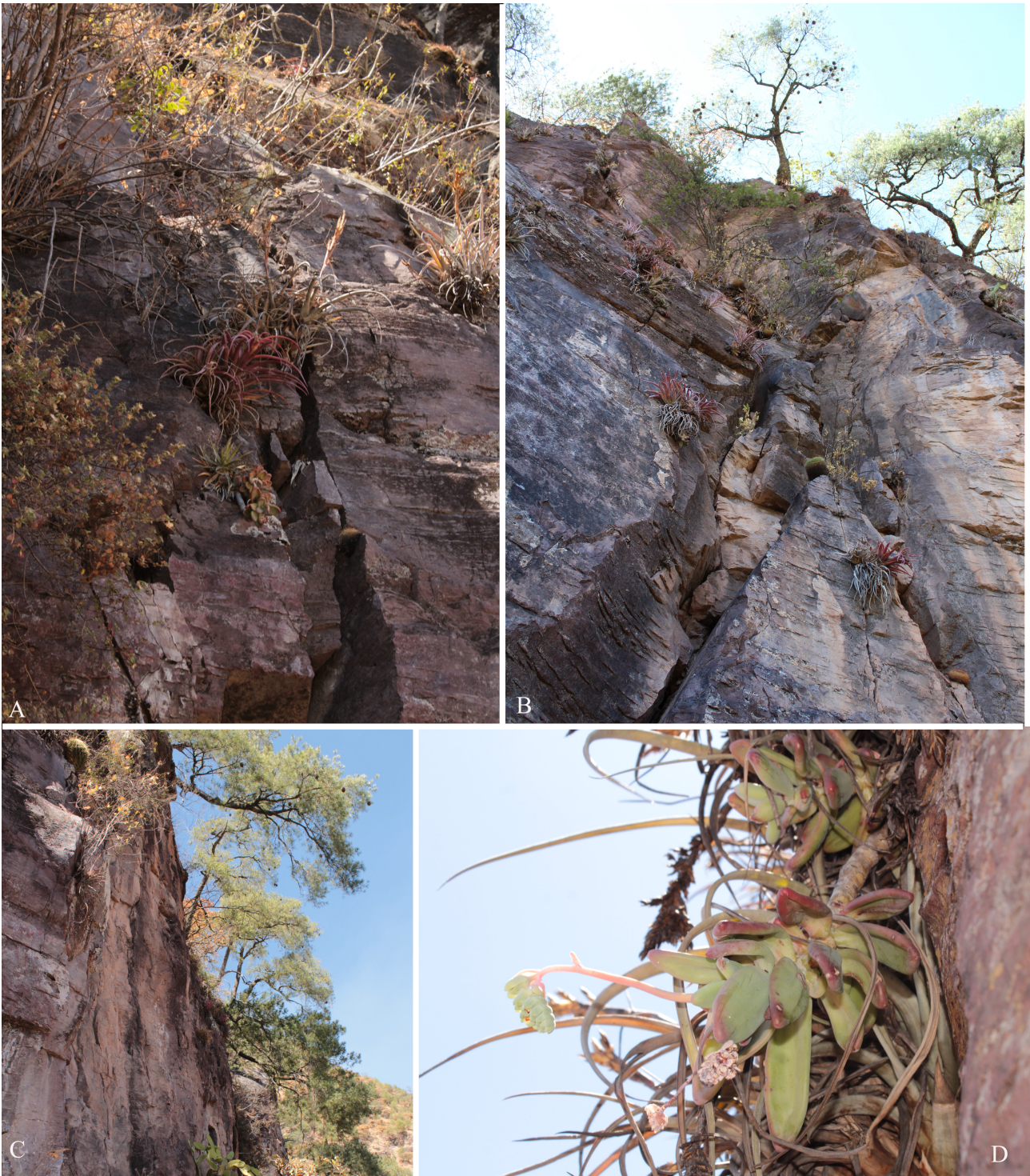


FIGURE 4. Habitat (A–C) and habit (D) of *Pachyphytum odam* Art. Castro & P. Carrillo.

Phenology:—*Pachyphytum odam* flowers and fruits in March. However, under cultivation in Durango city, the plants began to flower as early as December and continued until March.

Additional specimens examined:—**Mexico.** Durango: Mezquital: La Muralla, Reserva Comunitaria del bosque de *Pinus maximartinezii*, 1733 m, 15 March 2021 (fl, fr), A. Castro-Castro *et al.* 4699 (CIIDIR, IBUG, MEXU).

Conservation status:—*Pachyphytum odam* is known from the type location, where we have documented approximately 30 mature individuals. Members of the O'dam nation, on whose land *P. odam* occurs, have informed us that the species is rare and that they are unaware of other populations. Based on AOO results and following the IUCN criteria B2 (area of occupancy estimated to be less than 10 km² and known to exist at only a single location), we preliminarily propose that it be designated as critically endangered (CR/B1a).

Etymology:—The specific epithet honors the O’dam people or Southern Tepehuán, on whose land the new species grows.

Vernacular name:—*Pachyphytum odam* is known to members of La Muralla community as *da’npakal*, an O’dam word that can be translated as bald, naked, or slippery, perhaps alluding to the glabrous leaves and stems.

Acknowledgments

We are grateful to the curators and staff of consulted herbaria. Thanks to the O’dam Community from Santa María de Ocotán y Xoconoxtle, Anexo La Muralla for the facilities provided. To Azalea Guerra, Daniel Piñero, Jesús G. González, Laura Figueroa and Roberto Simental for their assistance during field work. The help of Gabriela Laines Rodríguez and José Ricardo Alanís Ayala in maintaining the living collections is greatly appreciated. We thank Nicodemo G. Passalacqua and an anonymous reviewer for suggestions to improve the manuscript. The research was funded by the Instituto Politécnico Nacional through the project Richness and geographic distribution of the Crassulaceae family in the state of Durango, Mexico (SIP-2020-0993), and California Academy of the Sciences.

References

- Bachman, S., Moat, J., Hill, A., de la Torre, J. & Scott, B. (2011) Supporting red list threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 111–126.
<http://dx.doi.org/10.3897/zookeys.150.2109>
- Cabrera-Luna, J., Serrano-Cárdenas, V. & Pelz-Marín, R. (2007) Plantas comercializadas como ornamentales decembrinas en 12 municipios de Querétaro, México. *Polibotánica* 24: 117–138.
- Carrillo-Reyes, P., Sosa, V. & Mort, M.E. (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.
<https://doi.org/10.1016/j.ympev.2009.05.022>
- de Candolle, A.P. (1828) Crassulaceae. *Prodromus Systematis Naturalis Regni Vegetabilis* 3: 381–414.
- de la Cruz-López, L.E., Vergara-Silva, F., Reyes-Santiago, J., Espino, G., Carrillo-Reyes, P. & Kuzmina, M. (2019) Phylogenetic relationships of *Echeveria* (Crassulaceae) and related genera from Mexico, based on three DNA barcoding loci. *Phytotaxa* 422: 33–57.
<https://doi.org/10.11646/phytotaxa.422.1.3>
- Fedde, F. (1937) I. E. Wendermann: Neue sukkulenten aus dem Botanischen Garten Berlin-Dahlem. II. *Repertorium Specierum Novarum Regni Vegetabilis* 42: 1–7.
- González-Elizondo, M., González-Elizondo, M.S., Ruacho-González, L. & Molina-Olvera, M. (2011) *Pinus maximartinezii* Rzed. (Pinaceae), primer registro para Durango, segunda localidad para la especie. *Acta Botanica Mexicana* 96: 33–48.
<https://doi.org/10.21829/abm96.2011.257>
- Gries, C., Gilbert, E.E. & Franz, N.M. (2014) Symbiota – A virtual platform for creating voucher-based biodiversity information communities. *Biodiversity Data Journal* 2: e1114.
<https://doi.org/10.3897/BDJ.2.e1114>
- Hijmans, R.J., Guarino, L., Bussink, C., Mathur, P., Cruz, M., Barrantes, I. & Rojas, E. (2004) *DIVA-GIS versión 4. Un sistema de información geográfica para el análisis de distribución de especies: Manual*. Lima, Perú: Centro Internacional de la Papa, Instituto Internacional de Recursos Genéticos Vegetales.
- IBUNAM (2022) *Pachyphytum*. Herbario Nacional de México (MEXU), Plantas Vasculares. Portal de Datos Abiertos UNAM Colecciones Universitarias (online), Mexico, Universidad Nacional Autónoma de México. Available from: <https://datosabiertos.unam.mx/biodiversidad/> (accessed: 6 December 2023).
- INEGI (2010) Archivo histórico de localidades geoestadísticas. Instituto Nacional de Estadística y Geografía. Available from: <https://www.inegi.org.mx/> (accessed: 6 December 2023).
- IUCN (2022) *Guidelines for using the IUCN Red List Categories and Criteria*. Version 15. Standards and Petitions Committee. Available from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> (accessed: 6 December 2023).
- Keith, D.A. (1998) An evaluation and modification of World Conservation Union Red List Criteria for classification of extinction risk in vascular plants. *Conservation Biology* 12: 1076–1090.

<https://doi.org/10.1046/j.1523-1739.1998.97202.x>

- Kimnach, M. (2010) Notes on Crassulaceae: 2. *Cactus & Succulent Journal of America* 82: 122–125.
<http://dx.doi.org/10.2985/015.082.0306>
- Klotzsch, J.F. (1841) Einer neuen mexikanischen Pflanze *Pachyphytum bracteosum*. *Allgemeine Gartenzeitung* 9: 9–10.
- Meyrán, J. (2019) *Las Crasuláceas de México Volumen II (2002-2019)*. Palabra en Vuelo, S.A. de C.V., Ciudad de México.
- Moran, R. (1963) *Pachyphytum brevifolium* Rose and *P. glutinicaule*, a new species from Hidalgo, Mexico. *Cactus and Succulent Journal* 35: 35–41.
- Moran, R. (1967) *Pachyphytum kimnachii*, a new species from San Luis Potosí. *Cactus and Succulent Journal* 39: 204–206.
- Moran, R. (1968) New subgeneric groups in *Echeveria* and *Pachyphytum*. *Cactus and Succulent Journal of America* 40: 36–42.
- Moran, R. (1971) *Pachyphytum fittkaui*, a new species from Guanajuato, Mexico. *Cactus and Succulent Journal* 43: 26–32.
- Morrone, J.J., Escalante, T. & Rodríguez-Tapia, G. (2017) Mexican biogeographic provinces: Map and shapefiles. *Zootaxa* 4277: 277–279.
<https://doi.org/10.11646/zootaxa.4277.2.8>
- Ortiz-Brunel, J.P., Munguía-Lino, G., Castro-Castro, A. & Rodríguez, A. (2021) Biogeographic analysis of the American genus *Echeandia* (Agavoideae: Asparagaceae). *Revista Mexicana de Biodiversidad* 92: e923739.
<https://doi.org/10.22201/ib.20078706e.2021.92.3739>
- Pérez-Calix, E. & Glass, C. (1999) *Pachyphytum brevifolium* Rose (Crassulaceae) a un siglo de su descubrimiento y *Pachyphytum garciae*, una especie nueva del centro de México. *Acta Botanica Mexicana* 48: 1–10.
<https://doi.org/10.21829/abm48.1999.829>
- Pérez-Calix, E., García, R.I. & Cházaro, B.M. (2008) Una nueva especie de *Pachyphytum* (Crassulaceae) para la flora de Jalisco, México. *Acta Botanica Mexicana* 83: 63–68.
<https://doi.org/10.21829/abm83.2008.1061>
- Pérez-Calix, E. & Torres-Colín, R. (2018) *Pachyphytum rogeliocardenasii* (Crassulaceae), a new species from northwestern Querétaro, Mexico. *Phytotaxa* 348: 56–62.
<https://doi.org/10.11646/phytotaxa.348.1.7>
- QGIS Development Team (2022) QGIS v. 3.24 Geographic Information System. QGIS Association. Available from: <http://www.qgis.org> (accessed: 6 December 2023).
- Reyes-Santiago, J., Pérez, J. & Brachet, C. (2004) *Echeveria cuicatecana*, una nueva especie para el estado de Oaxaca, México. *Cactáceas y Suculentas Mexicanas* 49: 80–84.
- Reyes-Santiago, J., de la Cruz-López, L.E., Kuzmina, M. & Vergara-Silva, F. (2019) Morphological and molecular diagnostic characters reveal a new species of *Pachyphytum* (Crassulaceae). *Haseltonia* 26: 14–22.
<https://doi.org/10.2985/026.026.0103>
- Reyes-Santiago, J., Etter, J., Kristen, M. & de la Cruz-López, L.E. (2020) *Pachyphytum huastecanum* (Crassulaceae), a new species from the Huasteca Canyon, Nuevo León, Mexico. *Cactus and Succulent Journal* 92: 141–147.
<https://doi.org/10.2985/015.092.0207>
- Rzedowski, J. (1964) Una especie nueva de pino piñonero del estado de Zacatecas (México). *Ciencia* 23: 17–20.
- Rzedowski, J. (1990) Vegetación Potencial. IV.8.2. Atlas Nacional de México. Vol II. Escala 1:4000000. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Available from: http://conabio.gob.mx/informacion/metadatos/gis/vpr4mgw.xml?_xsl=/db/metadatos/xsl/fgdc_html.xsl&_indent=no (accessed: 6 December 2023).
- Rzedowski, J. (2008) *Vegetación potencial*. Catálogo de metadatos geográficos. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico City. Available from: http://conabio.gob.mx/informacion/metadatos/gis/vpr4mgw.xml?_xsl=/db/metadatos/xsl/fgdc_html.xsl&_indent=no (accessed: 6 December 2023).
- Salm-Dyck, J.F. (1854) Beschreibung einer neuen mexikanischen Pflanze *Diotostemon hookeri*. *Allgemeine Gartenzeitung* 22: 265–266.
- Sánchez-Escalante, J.J. & Gilbert, E.E. (2019) Red de herbarios del noroeste de México: un esfuerzo colaborativo entre botánicos mexicanos. *Arido-Ciencia* 3: 21–35.
- SEMARNAT. (2019) Modificación del Anexo Normativo III, Lista de especies en riesgo de la Norma Oficial Mexicana NOM-059-SEMARNAT-2010, Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo, publicada el 30 de diciembre de 2010. *Diario Oficial de la Federación* 11: 32–134. Available from: https://www.dof.gob.mx/index_111.php?year=2019&month=11&day=14 (accessed: 6 December 2023).
- Simpson, M.G. (2006) *Plant systematics*. Elsevier Academic Press, Massachusetts.
- Sosa, V., Vásquez-Cruz, M. & Villarreal-Quintanilla, J.A. (2020) Influence of climate stability on endemism of the vascular plants of the Chihuahuan Desert. *Journal of Arid Environments* 177: 104139.
<https://doi.org/10.1016/j.jaridenv.2020.104139>

- Thiede, J. (1995) Quantitative phytogeography, species richness, and evolution of American Crassulaceae. *In*: Hart, H. 't & Eggli, U. (Eds.) *Evolution and systematics of the Crassulaceae*. Backhuys Publishers, Leiden, pp. 89–123.
- Thiede, J. (2003) *Pachyphytum*. *In*: Eggli, U. (Ed.) *Crassulaceae. Illustrated handbook of succulent plants*. Springer, Berlin, pp. 190–195.
- Thiede, J. & Eggli, U. (2007) Crassulaceae. *In*: Kubitzki, K. (Ed.) *The Families and Genera of Vascular Plants*. Springer, Hamburg, pp. 83–118.
- Vázquez-Cotero, C., Sosa, V. & Carrillo-Reyes, P. (2017) Phylogenetic position of *Echeveria heterosepala* (Crassulaceae): a rare species with diagnostic characters of *Pachyphytum*. *Botanical Sciences* 95 (3): 515–526.
<https://doi.org/10.17129/botsci.1190>
- Walther, E. (1931) Genus *Pachyphytum*. *Journal of the Cactus and Succulent Society of America* 3: 9–13.
- Walther, E. (1937) *Pachyphytum viride*, a new species. *Cactus and Succulent Journal* 8: 210–211.