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RESEARCH ARTICLE

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Serpocaulon × *manizalense*: a new hybrid between simple- and pinnate-leaved species of *Serpocaulon* (*Polypodiaceae*) from Colombia

D. Sanín[1], V. Torrez[2]

Key words

endangered fern
hybridization
multivariate analyses
Serpocaulon adnatum
Serpocaulon levigatum

Abstract During a revision of *Serpocaulon* from Colombia, a new hybrid was found between *S. adnatum* and *S. levigatum* near to Manizales city, which is described and illustrated herein. Qualitative and quantitative spore and macro-morphological characters were evaluated using principal component analyses to distinguish the new taxon. Our results suggest that the perispore with leasura, lamina width, rhizome diameter, blade dissection and number of pinnae are important characters to distinguish *S.* × *manizalense*. This is the first record of a hybrid between a simple and pinnate-leaved species in *Serpocaulon,* which is considered to be Critically Endangered (CR).

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INTRODUCTION

Serpocaulon A.R.Sm. is a Neotropical genus of *Polypodiaceae* with 42 species and three known hybrids (Smith et al. 2006, Labiak & Prado 2008, Rojas-Alvarado & Chaves-Fallas 2013, Schwartsburd & Smith 2013, Sanín 2014). The genus is characterized by a suite of morphological characters that includes long-creeping rhizomes, clathrate scales, veins regularly anastomosing (goniophlebioid), and areoles chevron-shaped with a single, free, included veinlet (Smith et al. 2006).

The two known hybrid taxa are *Serpocaulon* × *pubescens* (Rosenst.) Schwartsb. & A.R.Sm.) (Schwartsburd & Smith 2013), *S.* × *sessilipinnum* A.Rojas & J.M.Chaves (Rojas-Alvarado & Chaves-Fallas 2013), and one other taxon is often suggested as being of hybrid origin: *S. semipinnatifidum* (Fée) A.R.Sm. (Tryon & Stolze 1993, Moran 1995). However, there is the possibility to find more hybrids mainly between *S. levigatum* and others Andean species (Tryon & Stolze 1993, Moran 1995, Sanín 2011).

During a review of *Serpocaulon* from Colombia, a new hybrid was found co-occurring with *S. adnatum* (Kunze ex Klotzsch) A.R.Sm., and *S. levigatum* (Cav.) A.R.Sm. Considering that hybrids occur in areas that were subject to extreme changes where the parents used to be or are present (Rieseberg 1997), and that they have intermediate characters to their parental taxa (Moran & Watkins 2004), we presume that *S. adnatum* and *S. levigatum* are the putative parental taxa of the new hybrid, which also slightly resembles *S. semipinnatifidum*, of which no records are known from the area. Our study aims to describe the new hybrid and distinguish it from its putative parents and *S. semipinnatifidum*.

[1] Botanic Garden Meise, Bouchout Domain, Nieuwelaan 38, 1860 Meise, Belgium; corresponding author e-mail: dav.sanin@gmail.com.
[2] Plant Conservation and Population Biology, KU Leuven University, Kasteelpark Arenberg 31, B-3001, Heverlee, Belgium; torflorvania@gmail.com.

MATERIALS AND METHODS

Morphological sampling and characters

To discriminate the new hybrid, 411 herbarium specimens of *Serpocaulon adnatum* (133)*, S. levigatum* (222), *S. semipinnatifidum* (54), and the new hybrid (2) were selected from the herbaria CAUP, CHOCO, COL, CUVC, FAUC, FMB, HUA, HUQ, JAUM, MEDEL, MO, NY, PSO, and TOLI. Each studied specimen was sampled from a different individual.

Serpocaulon adnatum and *S. levigatum* were included in the analyses as they were found co-existing with the new hybrid. *Serpocaulon semipinnatifidum* was not found to co-exist with them, but it was included in the analyses as it can be confused with the new hybrid. The putative parents suggested for *S. semipinnatifidum*, in combination with *S. levigatum*, *S. funckii* (Mett.) A.R.Sm. (Moran 1995) and *S. lasiopus* (Klotzsch) A.R.Sm. (Tryon & Stolze 1993), were excluded from the analysis as they were not found to co-exist with the new hybrid. Furthermore, they are not recorded in the Caldas department (Fraume et al. 1990, Sanín & Duque-Castrillón 2006, Sanín et al. 2006, 2008, Álvarez-Mejía et al. 2007, Sanín 2011).

For morphometric analyses, 38 specimens were used as operational taxonomic units (OTU), representing the entire geographical range and the morphological variability within each taxon. A total of 59 morphological characters were measured, from which 35 were qualitative and 24 were quantitative. From these quantitative characters, eight were spore characters and 16 were macro-morphological characters.

The analysed spore characters are equatorial axis, length of aperture, polar axis, endospore, exospore, central verrucae, verrucae height and width. The spore description follows Ramírez-Valencia et al. (2013). The macro-morphological characters are rhizome diameter, rhizome scale length and width, phyllopodia distance, petiole length, lamina length and width, number of pinnae, lamina scale length and width. Additionally, we measured for the medial pinna length and width, the number of areolae and sori between the principal vein and the costa, and along the principal vein and the costa. For *S. levigatum*, which has a simple lamina, these characters were measured for the entire lamina. The macro-morphology description follows Lellinger (2002).

Numerical and statistical analyses

Quantitative characters were analysed by range and median values. Principal component analyses (PCA) were based on quantitative values of spore and macro-morphological characters. PCA results were used to support distinctions among the taxa. These analyses were performed using R (R Development Core Team 2013).

Conservation status

The conservation status of the new hybrid was assessed by applying the IUCN Red List Categories and Criteria (IUCN 2001).

RESULTS

Principal component analyses

Spore characters (Table 1)

The first three components accounted for 80 % of the total variance. The first principal component had high contributing loading values from verrucae height, verrucae width, central verruca, and polar axis. The second component had high contributing loadings from the endospore, exospore, central verrucae, and verrucae height. Finally, the third component had high contributing loadings from polar axis, equatorial axis, exospore and endospore.

In the scatterplot against the first two components (Fig. 1), the OTUs are arranged in loose and slightly overlapping groups, corresponding to *S. levigatum*, *S. semipinnatifidum* and *S.* × *manizalense*. Despite the overlap, it is possible to recognize the new hybrid (*S.* × *manizalense*) between *S. levigatum* and *S. adnatum*. In addition, the spores of the other hybrid (*S. semipinnatifidum*) are in a cluster separate from the other taxa.

Macro-morphological characters (Table 2)

The first three components accounted for 68.7 % of the total variance observed. The first principal component had high contributing loading values from petiole length, lamina width, rhizome diameter and number of pinnae, among the four most important. The second component had high contributing loadings from medial pinna width and lamina length. Finally, the third component had high contributing loadings from rhizome scale length, rhizome scale width, rhizome diameter, and lamina length.

In the scatterplot of the first two components, the OTUs are arranged in four different clusters, each representing a different taxon (Fig. 2). This result allowed us to easily characterize the four taxa and support the description of the new hybrid (*S.* × *manizalense*). Nevertheless, *S. levigatum* and *S. semipinnatifidum* are slightly overlapping.

Table 1 Summary of the principal component weights for the spore characters. In **bold**, morphological characters showing the highest values.

Character	Axes 1	Axes 2	Axes 3
Equatorial axis	0.607	-0.538	**0.418**
Polar axis	**0.715**	-0.285	**0.515**
Endospore	0.362	**0.791**	**0.110**
Exospore	0.365	**0.717**	**0.191**
Central verrucae	**0.906**	**0.103**	-0.184
Verrucae width	**0.910**	-0.021	-0.154
Verrucae height	**0.914**	**0.072**	-0.109
Aperture longitude	0.547	-0.289	-0.594

Table 2 Summary of the principal component weights for the macro-morphological characters. In **bold**, morphological characters showing the highest values.

Character	Axes 1	Axes 2	Axes 3
Rhizome diameter	**0.899**	-0.229	**0.135**
Rhizome scale length	0.766	-0.100	**0.460**
Rhizome scale width	0.706	-0.072	**0.404**
Phyllopodia distance	0.142	-0.029	0.012
Petiole length	**0.925**	-0.163	0.089
Number of pinnae	**0.895**	-0.265	0.023
Lamina length	0.856	**0.268**	**0.122**
Lamina width	**0.917**	-0.271	0.024
Pinna media length	0.803	**0.473**	-0.027
Pinna media width	0.752	**0.374**	-0.067

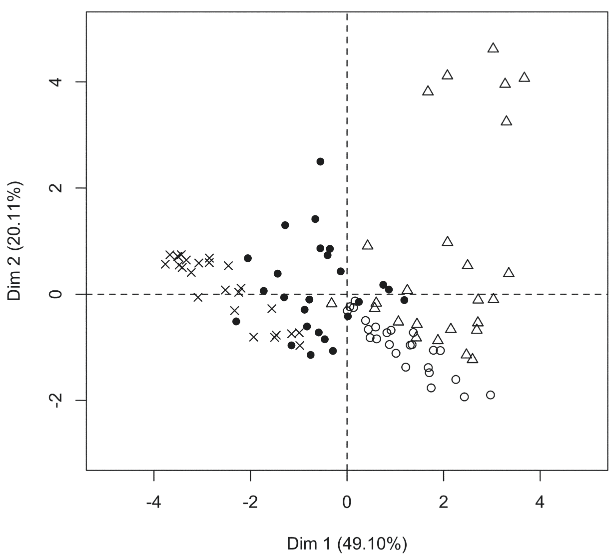

Fig. 1 Plot of the first two components of the PCA from the spore morphology. *Serpocaulon* × *manizalense* (●); *S. semipinnatifidum* (○); *S. adnatum* (×); *S. levigatum* (△).

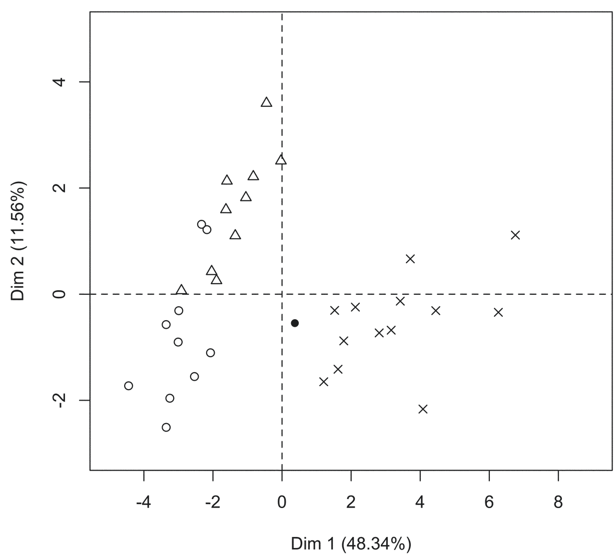

Fig. 2 Plot of the first two component of the PCA from the macro-morphology. *Serpocaulon* × *manizalense* (●); *S. semipinnatifidum* (○); *S. adnatum* (×); *S. levigatum* (△).

DISCUSSION

Spore characteristics of the hybrid

The slight overlap of *S. levigatum*, *S. semipinnatifidum* and *S.* × *manizalense* in the PCA of spore morphology, could be explained by the fact that *S. levigatum* is a parent of *S. semipinnatifidum* (Tryon & Stolze 1993, Moran 1995, Sanín 2011) and with the present results we propose that it is also one of the parental species of the new hybrid. In addition, the new hybrid is arranged between *S. levigatum* and *S. adnatum* (Fig. 1), both proposed as putative parental species of *S.* × *manizalense*.

According to the PCA results, the most important spore characters to differentiate the new hybrid are the shape and ornamentation of the spores, in particular the verrucae (Table 1). Similarly, Ramírez-Valencia et al. (2013) reported these spore characters as useful to distinguish 21 species of *Serpocaulon* from Colombia.

Interestingly, the described hybrid has well-formed spores (see description of the hybrid), an unusual characteristic in fern hybrids. Usually, fern hybrids have malformed spores (Haufler 2008, Sharpe et al. 2010). However, *S.* × *manizalense* is not the first described hybrid with well-formed spores. Such a characteristic has been described in other fern hybrid taxa such as *Polystichum* Roth. (Mullenniex et al. 1998), *Asplenium* L. (Morzenti 1967), *Polypodium* L. (Haufler et al. 1995), and also in *Serpocaulon* (Rojas-Alvarado & Chaves-Fallas 2013).

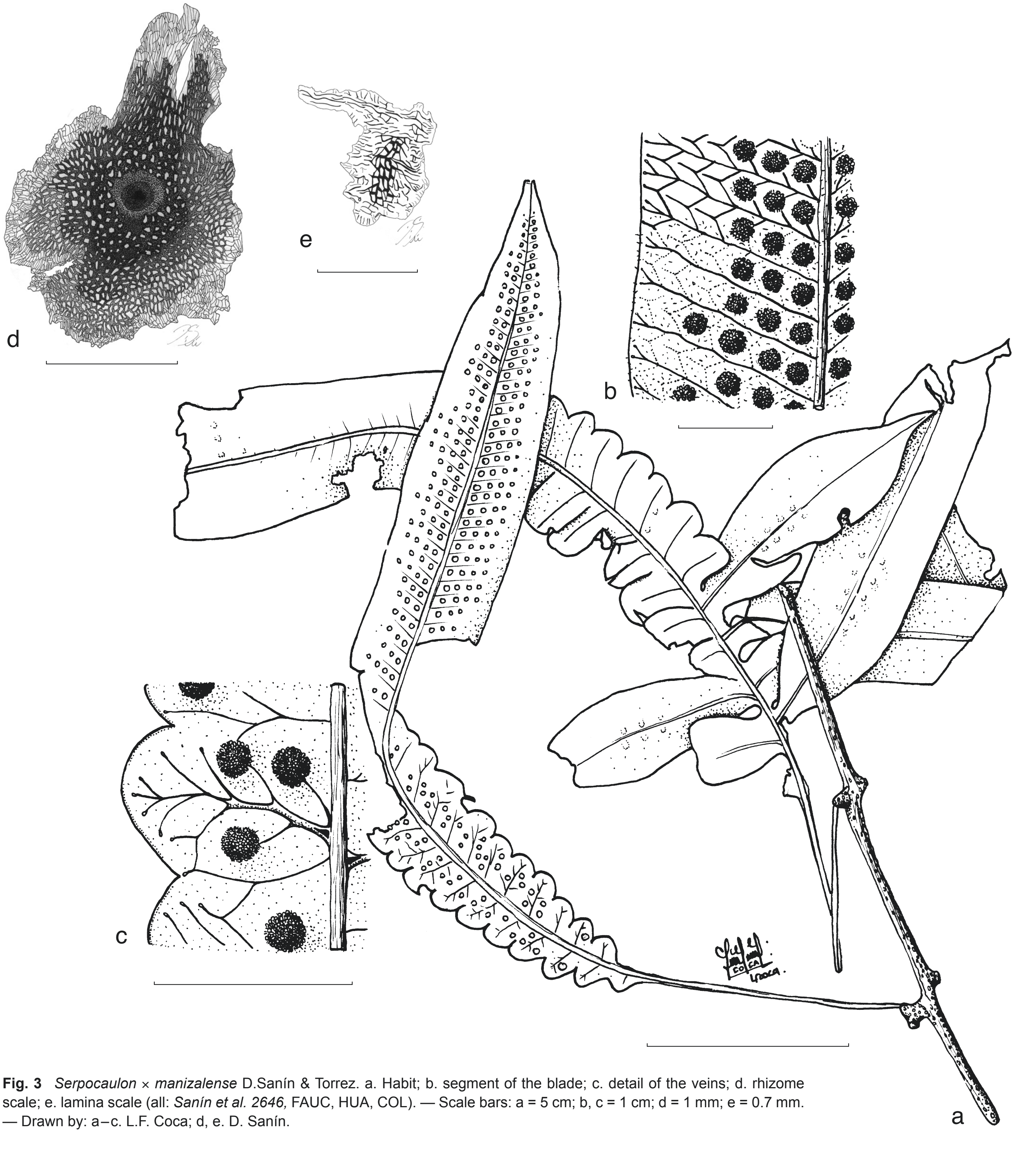

Fig. 3 *Serpocaulon* × *manizalense* D.Sanín & Torrez. a. Habit; b. segment of the blade; c. detail of the veins; d. rhizome scale; e. lamina scale (all: *Sanín et al. 2646,* FAUC, HUA, COL). — Scale bars: a = 5 cm; b, c = 1 cm; d = 1 mm; e = 0.7 mm. — Drawn by: a–c. L.F. Coca; d, e. D. Sanín.

Macro-morphology of the hybrid

Some of the most frequently used characters to distinguish *Serpocaulon* species are: rhizome diameter, laminar length and width, petiole length, rhizome scale length and width (Lellinger 1989, Tryon & Stolze 1993, Moran 1995, Labiak & Prado 2008, Sanín 2014). However, in the present study other less frequently used characters such as number of pinnae or segments, medial pinnae length and width appeared to be important to distinguish the new hybrid.

The PCA analysis of the macro-morphology resulted in better-resolved groups than that of the spore characters, and only *S. levigatum* and *S. semipinnatifidum* are overlapping. This is not surprising, since it was reported that *S. levigatum* is the parental taxon of *S. semipinnatifidum* (Tryon & Stolze 1993, Moran 1995, Sanín 2011), while the other parental taxon remains uncertain. Moran (1995) proposed that the other putative parent may be *S. funckii* for the north of the Andes hybrids (Colombia and Venezuela). However, Tryon & Stolze (1993) suggested that *S. lasiopus* may be the other putative parental taxon of *S. semipinnatifidum* for the hybrids located in Peru.

Hybrid habitat

Despite the extensive botanical exploration of the Chinchiná basin river (Fraume et al. 1990, Orrego et al. 2004, Sanín & Duque-Castrillón 2006, Sanín et al. 2006, 2008, Álvarez-Mejía et al. 2007), there is only one wild population of *S.* × *manizalensis* known, and another single plant propagated by rhizome, which has been maintained for conservational purposes in the JBOUC.

Frequently, the formation of a hybrid is triggered by an extreme change in the habitat of the parental taxa (Rieseberg 1997, Rieseberg et al. 2006, Kentner & Mesler 2000).

Thus, most of the hybrids appear in highly disturbed areas such as road cuts (Barrington 1985). Probably, the generation of *S.* × *manizalense* was promoted by the conversion of the natural area to a landfill, which has been opened since 1991.

TAXONOMIC TREATMENT

Serpocaulon* × *manizalense D.Sanín & Torrez, *hybrid nov.* — Fig. 3, 4

Hybrida inculta e *Serpocaulon adnatum* et *S. levigatum* genita, epiphytica et terrestrium; a *S. semipinnatifidum* differ rhizoma longe 5–5.5 mm (versus 1.7(–2.9–)4.7 mm), lamina longe 25(–30–)33 per 8(–28–)30 cm (versus 15(–24.7–)32 per 1.2(–4–)9) cm, areolis magis numerosis secus pinna basal 1–5 series (versus 1–3 series). — Type: *Sanín et al. 2646* (holo FAUC; iso COL, HUA), Colombia, Caldas, Manizales, flanco occidental de la Cordillera Central, vía a Neira, cerca del Relleno Sanitario La Esmeralda, zona a la derecha que se pronostica conservar en la ampliación del Relleno [N05° 04'49" W75°30'27"], 2200 m, 3 Nov. 2008.

Etymology. The new hybrid is named after the city of Manizales and its people.

Plants terrestrial and epiphytic. *Rhizomes* 5–5.5 mm diam, long-creeping, dark brown to reddish, faintly farinose. Phyllopodia 7–7.3 cm apart. *Scales* 1.3(–2–)2.5 by 0.8(–1–)2.0 mm, appressed, with rounded bases and rounded to acute apices, ovate to ovate-lanceolate, dispersed along the rhizome, dark brown at centre, clathrate, hyaline at the margin. *Petioles* 10–12.2 cm, articulate, subterete, 1/2 length of blade, stramineous. *Laminae* 25(–30–)33 by 8(–28–)30 cm, simple with crenate margins to base and lanceolate shape or basally pinnate and ovate-lanceolate truncate shape, glabrous, rachis distally stramineous. *Pinnae* absent or up to 4 pairs, of irregular size, firm to coriaceous, proximally adnate, with 7 basal lobules that are attenuate, apex long-caudate to acute in the distal pinnae. Proximal pinnae 15.8–16.3 by 3.5–3.8 cm. *Veins* goniophlebioid, closed chevron-shape areoles 28–30 by 2–5 rows between the costae and pinna margins, with one included fertile veinlet or open, irregularly shaped with two included fertile veinlets. Laminar indument consisting of scales, 0.8–1 by 0.5–0.6 mm, acicular, bicolorous, to 9 cells wide. Sori in 1–5 rows between costae and margin. Spores 54.5–56.5 by 33.5–35.5 µm, well-formed, monolete, aperture 21.8–24.8 µm long, laesurae straight, ambit ellipsoid, plane-convex to concave-convex, ornamentation densely verrucate, verrucae 3–4 by 4.5–5.5 µm, regular in size and rounded, evenly distributed, exospore 1–1.5 µm, perispore 1.3–1.5 µm, sulcate.

Distribution & Ecology — *Serpocaulon* × *manizalense* occurs on the western slope of the Central Andean Cordillera of Colombia, near Manizales on the road to Neira, in the locality of La Esmeralda landfill (Fig. 5a, Map 1). It was found epiphytic on *Rhus striata* Ruíz & Pav. (*Anacardiaceae*) and terrestrial in secondary forests (Fig. 5b). In addition, the only *Serpocaulon* species found in the area were *S. adnatum* and *S. levigatum*. *Serpocaulon* × *manizalense* was collected fertile in November 2008, and also it was seen fertile in September 2013 from cultivated plants in the Caldas University Botanical Garden (JBOUC) (Fig. 5c–e).

Notes on related taxa — The characters of *S.* × *manizalense* that are crucial to distinguish it from *S. semipinnatifidum* are present in the rhizome, lamina, and spores (Table 3). The rhizome in *S.* × *manizalense* is wider than in *S. semipinnatifidum*. The blade dissection in *S.* × *manizalense* is lobate to proximally pinnate (Fig. 3, 6), whereas *S. semipinnatifidum* is lobate to proximally pinnatisect (Fig. 6). Frequently, the lamina length of

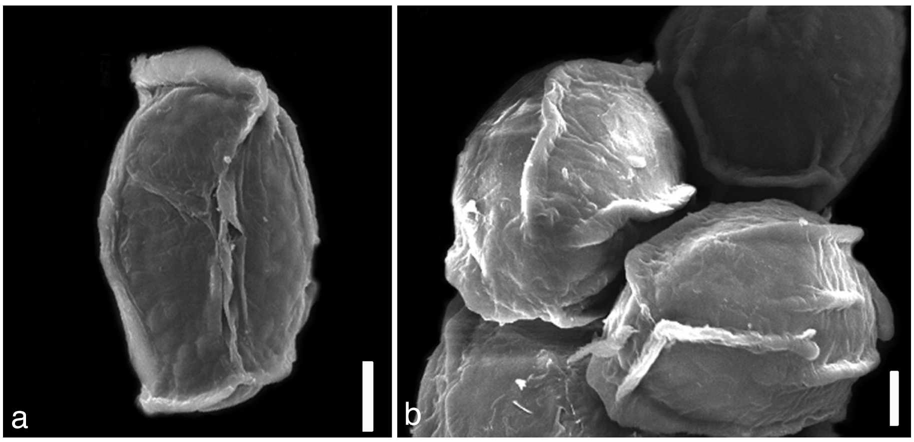

Fig. 4 Scanning electron micrographs of spores of *S.* × *manizalense* D.Sanín & Torrez, 1200×, 15 kV. a. Lateral view; b. clustered spores with visible leasura in the perispore (all: *Sanín et al. 2646,* FAUC). — Scale bars = 10 µm.

Fig. 5 Ecosystem, location, and propagated plant of the type collection. a. Ecosystem of *S.* × *manizalense* D.Sanín & Torrez; b. location of the type collection; c–e. asexual cultivated plants of *S.* × *manizalense*.

Table 3 Contrasting characters between *S.* × *manizalense*, *S. semipinnatifidum, S. adnatum*, and *S. levigatum*. Minimum, median, and maximum values are given for quantitative characters.

Character	*S.* × *manizalense*	*S. semipinnatifidum*	*S. adnatum*	*S. levigatum*
Rhizome diameter (mm)	5–5.5	1.7(–2.9–)4.7	4(–7–)10	1.6(–3.3–)4.7
Scale length (mm)	1.3(–2–)2.5	0.8(–1–)1.8	1(–2–)3	1(–1.2–)1.7
Blade dissection	Lobated to proximally pinnate	Lobated to proximally pinnatisect	Pinnate	Simple
Lamina shape	Lanceolate (when it is simple) or ovate-lanceolate (when it is pinnate)	Lanceolate	Narrow to amply ovate	Ovate-lanceolate
Lamina length (cm)	25(–30–)33	15(–24.7–)32.5	20(–52–)88	5.7(–14–)26
Number of areoles between the costae and pinna margin	1–5	1–3	4(–6–)7	3(–4–)6
Perine with laesura	Present	Absent	Absent	Absent

Fig. 6 Silhouettes. a. *Serpocaulon* × *manizalense* (*Sanín et al. 2646*, FAUC, HUA, COL); b. *S. adnatum* (*Coca et al. 199*, FAUC); c. *S. levigatum* (*Sanín et al. 5124*, NY); d. *S. semipinnatifidum* (*Rodríguez et al. 6103*, HUA, NY). All plants collected in Colombia. — Scale bar = 10 cm.

Map 1 Distribution of *Serpocaulon* × *manizalense* D.Sanín & Torrez.

S. × *manizalense* is larger than of *S. semipinnatifidum* (Fig. 6). In addition, the species differ in the number of areoles between the costae and pinna margin, *S.* × *manizalense* has 1–5 areoles and *S. semipinnatifidum* has 1–3 areoles. The spores of *S.* × *manizalense* show a laesura in the perispore (Fig. 4), while the spores of *S. semipinnatifidum* do not have a laesura in the perispore (Ramírez-Valencia et al. 2013).

The most conspicuous intermediate characters between the putative parents and the new hybrid are the blade dissection and the number of pinnae in the lamina: pinnate with 4(–7–)10 pairs in *S. adnatum,* lobate to pinnate with up to 4 pinnae pairs in the hybrid, and a simple lamina in *S. levigatum* (Fig. 6). The rhizome diameter of *S.* × *manizalense* is intermediate between *S. adnatum* and *S. levigatum*. Less conspicuous, but also intermediate were the colour and rhizome scales length. The rhizome scales in *S. adnatum* are dark brown to nearly black with 1–3 mm long (Fig. 7), in *S. levigatum* are pale orange with 1–1.7 mm long (Fig. 7), whereas in *S.* × *manizalense* are pale orange to brown with 1.3–2.5 mm long (Fig. 7).

Conservation — IUCN Red List Category: Critically Endangered [CR B2a + D]. The EOO cannot be estimated for *S.* × *manizalense* because it is known from only one location. The AOO is 9 km^2, and it falls completely outside any protected and pristine area under the Colombian System of Protected Areas.

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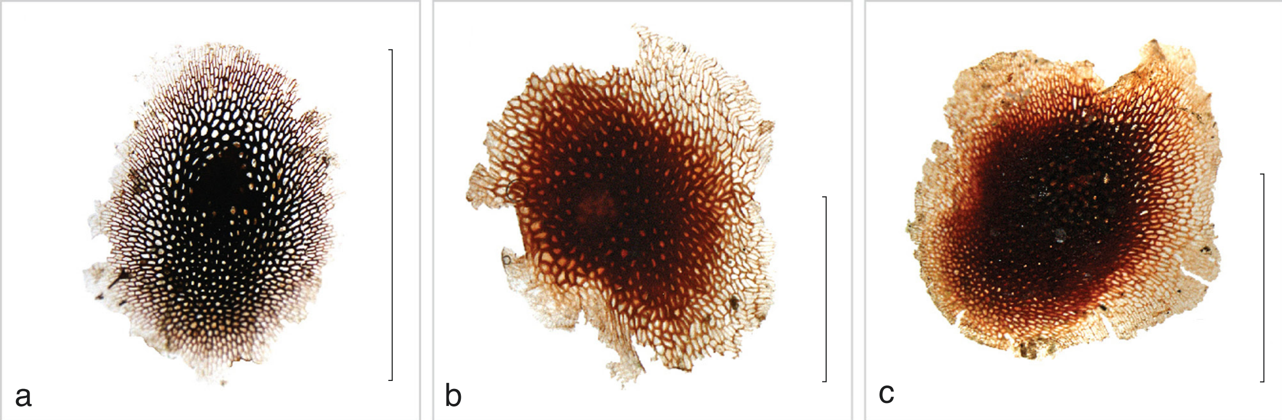

Fig. 7 Rhizome scales. a. *Serpocaulon adnatum*; b. *S.* × *manizalense*; c. *S. levigatum* (a. *Sanín et al. 3080,* FAUC; b. *Sanín et al. 2646,* FAUC, HUA, COL; c. *Sanín et al. 3315,* FAUC). — Scale bars: a = 2.5 mm; b = 1 mm; c = 1.5 mm.

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