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***Pinguicula pygmaea* (Lentibulariaceae), a new annual gypsicolous species from Oaxaca State, Mexico**

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Abstract

Pinguicula pygmaea (Lentibulariaceae), a new species from the Sierra Madre del Sur of western Oaxaca, Mexico is described and illustrated. The morphological characteristics distinguishing this new species from other similar species are discussed, together with its distribution and ecology.

Resumen

Se describe e ilustra *Pinguicula pygmaea* (Lentibulariaceae), una nueva especie de la Sierra Madre del Sur de Oaxaca Occidental, México. Se discuten las características morfológicas que distinguen esta nueva especie de otras especies similares, así como su distribución y ecología.

Key words: butterworts, carnivorous plant, gypsophile, taxonomy

Introduction

The genus *Pinguicula* Linnaeus (1753: 17) is one of three genera in the carnivorous plant family Lentibulariaceae (Lamiales) and comprises c. 95 species, of which about 40% occur in Mexico (Legendre 2000, Cieslak *et al.* 2005, Shimai & Kondo 2007, Lampard *et al.* 2016, Roccia *et al.* 2016). The state of Oaxaca in southern Mexico is home to thirteen species of *Pinguicula* (including the taxon newly described here), eight of which are endemic, the majority of them occurring on the Sierra Madre del Sur mountain range (Zamudio 2001, 2005, Zamudio & van Marm 2003, Lampard *et al.* 2016).

The greater part of Mexican *Pinguicula* species are perennial plants, surviving a winter dry dormancy as succulent, non-carnivorous “winter rosettes” or as compact, bulb-like subterranean rosettes (so-called “heterophyllous growth type”; Casper 1966, Roccia *et al.* 2016). However, a few homophyllous species evolved an annual life cycle in response to the seasonally dry climate: *Pinguicula crenatiloba* Candolle (1844: 30), *Pinguicula lilacina* Schlechtendal & Chamisso (1830: 94) [incl. *Pinguicula sharpii* Casper & Kondo (1977: 112); species concepts following Roccia *et al.* 2016 and Lampard *et al.* 2016], and *Pinguicula takakii* Zamudio & Rzedowski (1986: 260). These short-lived therophytes germinate towards the end of the rainy season and start to die back after anthesis and seed set, outlasting the dry season as seeds dispersed on the ground.

These ephemeral annual *Pinguicula* species are generally much smaller and more delicate plants than their perennial counterparts, with leaves translucent enough that one can see droplets of condensed water collected on the undersides of the leaves. Among these annuals, *P. crenatiloba* is one of the smallest species in the genus, usually only 3–4 cm tall in flower, rarely exceeding 7 cm in height, and bearing minute flowers with a corolla of just about 4.5–6 mm in length (Ernst 1961, Casper 1966, Lampard *et al.* 2016).

During expeditions to western Oaxaca state in 2003 and 2016, a minute and hitherto unknown annual species of *Pinguicula* was discovered and studied at three locations growing on gypsum soils. This taxon is described as a species new to science, based on comparative herbarium studies and observations made in the wild.

Material and Methods

Herbarium specimens (see also Appendix 1) were studied by at least one of the authors at IEB, M and MEXU (herbarium acronyms following Thiers 2016), field observations were performed by FR & ELR in Mexico in November 2003 and by FR in December 2003 and November 2016. The distribution map was created by DIVA GIS (Hijmans *et al.* 2005) using free spatial geodata for Mexico.

Description of the new species

Pinguicula pygmaea Rivadavia, E.L.Read & A.Fleischm., sp. nov. (Figs. 1–3)

Similar to *Pinguicula crenatiloba* DC. regarding habit, leaf shape, the bilabiate corolla with upper lip smaller than the lower lip, and the overall diminutive size, but differs from that species by entire corolla lobes (crenate to emarginate in *P. crenatiloba*), by the upper corolla lip only slightly separated from the lower lip, creating a short tubular throat (deeply bilabiate corolla, tubular corolla throat almost absent), by the three subequal lobes of the lower corolla lip (median lobe much larger than the two lateral ones), and by a spur which exceeds the corolla lower lip in length (spur shorter than to at maximum equal to the length of lower corolla lip).

Type:—MEXICO. Oaxaca: Municipio de Santo Domingo Tonalá, Highway 125, between Huajuapan and Tlacotepec, 1370 m, 20 November 2003, *Rivadavia & Read 1814* (holotype IEB!, isotype M!).

Small delicate annual herb, forming a lax rosette spread flat on the ground. Roots few, poorly developed, unbranched. Active green leaves 2–5, membranous, obovate to elliptic, 4–6(–8) mm long and 2.5–4(–5) mm wide; apex rounded, base cuneate, short petiolate; margins strongly involute in the distal 2/3 of the leaf; lamina upper surface densely covered with short-stalked adhesive and sessile digestive glands. Inflorescences 1-flowered, erect, densely covered with stalked-glands, 1–5(–7) scapes per plant; scapes slightly arcuate and (5–)10–25 mm long at anthesis, terete, up to 0.5 mm in diameter, straight, erect and prolonged to 30–65 mm in fruit. Calyx pentamerous, bilabiate, densely covered with glandular hairs on the outer surface; the three upper calyx lobes divided to 2/3 of their length, triangular, 1–1.5 mm long and 0.5–1 mm wide; the two lower calyx lobes fused to about 3/4 of their length, c. 2 mm long and 1 mm wide. Corolla pentamerous, bilabiate, tubular, white to very pale rose, white at the base of the corolla lobes near the throat, with yellowish-green mark on the palate at the base of the lower lip and inside the throat and spur; corolla (3–)3.5–5 mm long including the spur; upper corolla lip bilobate, smaller than the lower lip, lobes spreading, 1–1.5 × 0.5–1 mm, rectangular to ovate-elliptic in outline, apex obtuse to shallowly retuse; lower corolla lip distinctly trilobate, lobes subequal, 1–1.5(–2) mm × 1–1.5 mm, the lateral lobes only slightly smaller than the median lobe, ovate to circular in outline, apex obtuse, palate sparsely covered with short, subclavate to cylindrical, multicellular hairs c. 0.05–0.1 mm long; tubular throat widely open, very short, 0.5–0.7 mm long, up to 7 mm in diameter, conical to cylindrical; spur yellowish-green, narrowly conical to cylindrical, narrowed towards an acute or obtuse apex, 1–2.5(–3) mm long, 0.3–0.5 mm in diameter; corolla outer surface glabrous, except single scattered glandular hairs on the spur. Anthers 2, filaments falcate, white, c. 0.7 mm long and up to 0.2 mm wide, papillate, thecae subequal. Ovary subglobose, glandular; style short, subsessile, c. 0.5 mm long, stigma bilabiate, the lobes subequal, upper lobe scale like, c. 0.1 mm long, the lower lip much larger, c. 0.4 mm long, suborbicular, papillate, reddish pink. Capsule globose, to 1.5 mm in diameter, subequaling the persistent calyx lobes, wall membranous, capsule longitudinally bivalve. Seeds numerous, light brown, truncate-obovoid, testa reticulate.

Distribution:—*Pinguicula pygmaea* is known from only two localities just south of Santo Domingo Tonalá (c. 1370–1400 m elevation) and one just north of Santiago Juxtlahuaca (c. 1680 m elevation), along highway 125 between Huajuapan and Tlacotepec, in western Oaxaca state, Mexico. Although no further populations of *P. pygmaea* have been discovered (or specifically searched for) so far, it is likely that the species occurs in at least some of the numerous seemingly suitable habitats on gypsum hillsides observed in the vicinities of Tonalá and Juxtlahuaca (Fig. 2).

Conservation status:—Although very abundant at two of the three sites where it was observed, *P. pygmaea* does not occur within any protected area, and it is not guaranteed to occur in other apparently suitable habitats nearby. Moreover, easily accessible gypsum deposits are generally under potential threat from mining (IUCN Threats Classification: 3.2). Therefore, this new species is considered Vulnerable (VU D2) according to the criteria of IUCN (2012).

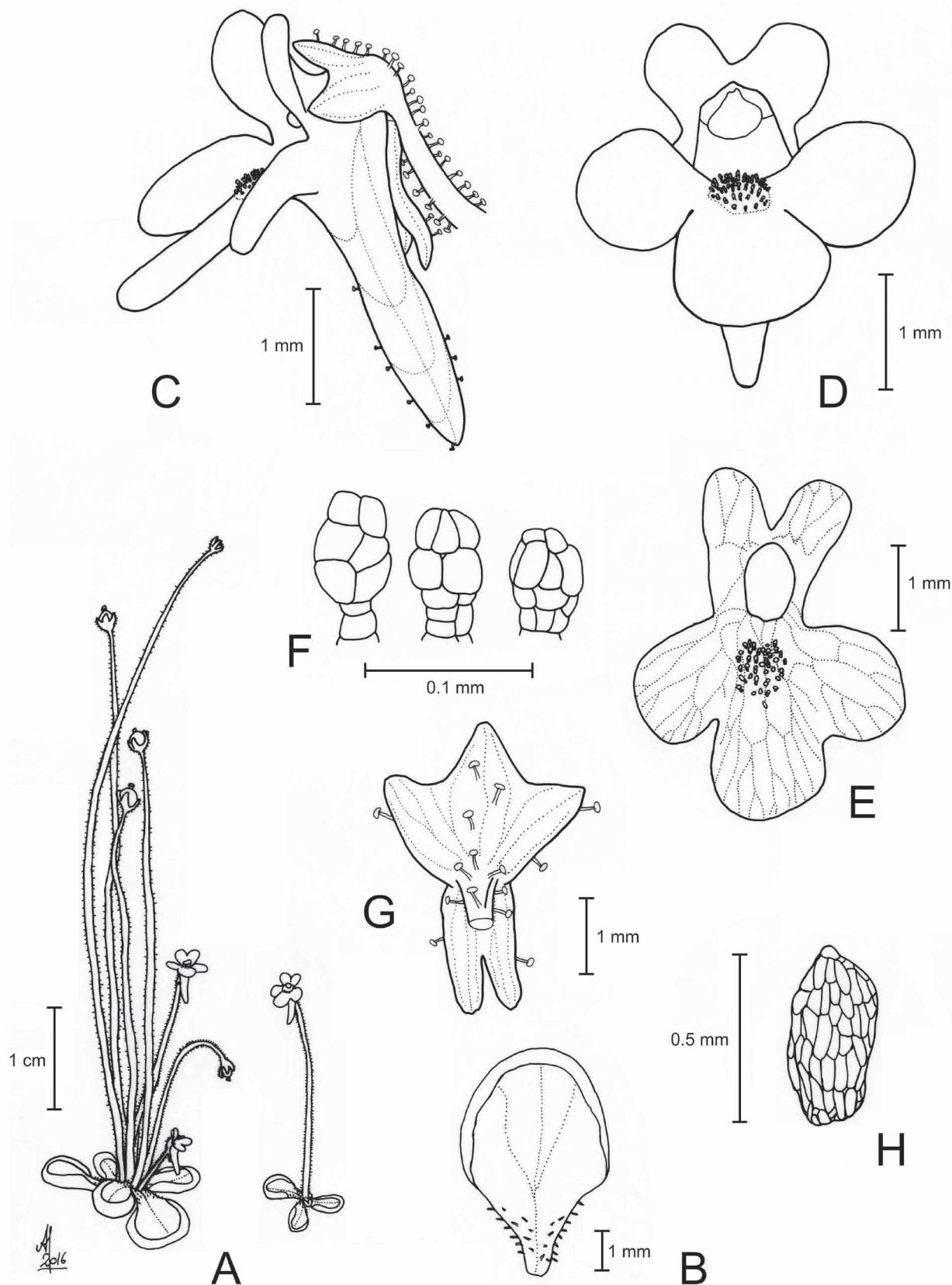


FIGURE 1. *Pinguicula pygmaea*. **A**, habit (left: specimen near the end of its growing cycle; right: specimen at the beginning of anthesis). **B**, leaf. **C**, corolla, side view. **D**, corolla, face view. **E**, corolla, flower preparation (spur dissected from the corolla). **F**, multiseriate hairs from corolla palate. **G**, calyx. **H**, seed. **A**, **B**, **G**, **H** from Rivadavia & Read 1814, **E**, **F** from Rivadavia et al. 2727, **C**, **D** from photographs of plants *in situ*. Drawing by A. Fleischmann.

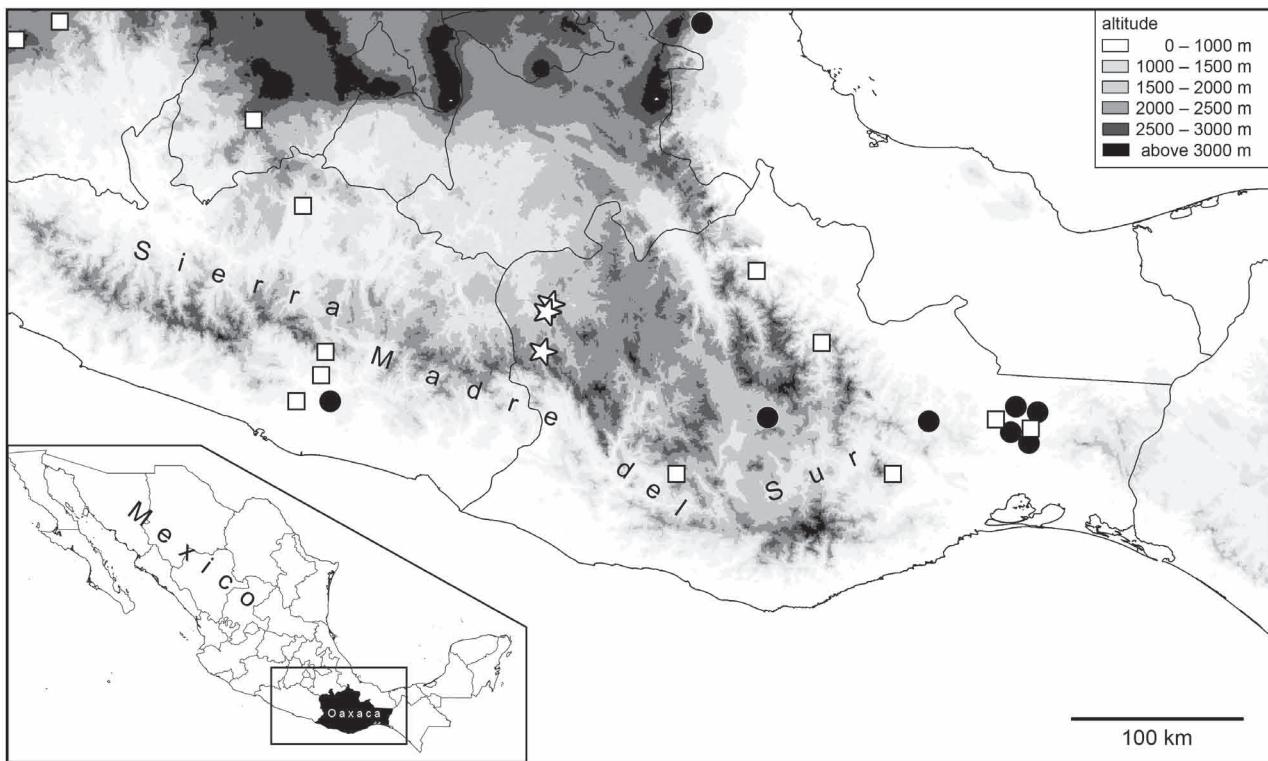


FIGURE 2. Distribution of *Pinguicula pygmaea* (white stars), of the related *P. crenatiloba* (white boxes), and the similarly annual *P. lilacina* (black dots) in southern Mexico (location data based on herbarium records and field observations). The fourth small Mexican annual species, *P. takakii*, is endemic to San Luis Potosí state, which is outside the range of this map.

Etymology:—The specific epithet “*pygmaea*” (pygmy) denotes the minute size of this delicate annual, which is among the smallest of all known *Pinguicula* species, only rivaled in its diminutive stature by the closely related *P. crenatiloba*, as well as by the only distantly related, Arctic circumpolar perennial *Pinguicula villosa* Linnaeus (1753: 17) and dwarf specimens of the annual *Pinguicula lusitanica* Linnaeus (1753: 17) from Atlantic western Europe and north-western Africa.

Habitat and ecology:—Annual therophyte and strictly gypsicolous. *Pinguicula pygmaea* grows on north-facing gypsum walls and hillsides in xeric shrubland, accompanied by the poikilohydric perennial (“resurrection plant”) *Selaginella* L., the perennial heterophyllous geophyte *Pinguicula heterophylla* Bentham (1840: 70), annuals such as *Centaurium* Hill (Gentianaceae), and xerophytic and geophytic perennial plants such as species of *Hechtia* Klotzsch (Bromeliaceae), *Agave* L. (Agavaceae), *Oxalis* L. (Oxalidaceae), *Aristolochia* L. (Aristolochiaceae), *Opuntia* Mill., *Neobuxbaumia mezcalensis* (Bravo) Backeb. (Cactaceae), *Fouquieria ochoterenae* Miranda (Fouquieriaceae), *Brahea dulcis* (Kunth) Mart. (Arecaceae), ferns, liverworts, and grasses. *Pinguicula pygmaea* is locally abundant at two of the three sites studied in early and late November on north-facing hillsides, growing in open gypsum soil. At the third site, only a small number of individuals was observed. At two of the three sites, *P. pygmaea* grows sympatrically with *P. heterophylla*. The type location was revisited in December 2003, three weeks after the species’ initial discovery, and almost all plants were already dead, possibly as a result of a frost event that occurred the night before, but not because of drought. The remaining annual species in Mexico (*P. lilacina*, *P. crenatiloba*, and *P. takakii*) have been observed alive and flowering well into the dry season at some locations (information from herbarium records, and from R. Resendiz Torreblanca, pers. comm.), as late as February. This suggests that, unlike *P. pygmaea*, these other species are seemingly unaffected by the light frosts of winter. It is suspected that cooler winter temperatures often allow these annuals to persist into the mid or late dry season thanks to a combination of condensation at night and shade resulting from the northern orientation of their habitats or from surrounding vegetation. Moreover, at least in the state of Oaxaca, *P. lilacina* and *P. crenatiloba* appear to occur at lower elevations (250–1000 m, see other specimens examined in Appendix 1 and Fig. 2) compared to *P. pygmaea* (1370–1680 m), hence will experience different climatic conditions. However, *P. lilacina*, *P. crenatiloba* and *P. takakii* apparently die off as the weather heats up and soils dry out late in the dry season, when the sun rises higher during spring (March to June), and before the rains return in late spring and

early summer (June to July). The Sierra Madre del Sur highlands of southern Mexico (Oaxaca, Guerrero and southern Michoacán) is rich in *Pinguicula* species, especially on its eastern portion in the state of Oaxaca. The high species diversity of *Pinguicula* (and also other species-rich montane plant genera) observed on certain Mexican mountain ranges has been explained by differing microclimates and especially a variety of edaphic conditions found in close proximity, ranging from limestone and gypsum to igneous and volcanic rock, resulting in many geographically close but fundamentally different habitat niches (Zamudio 2005, Mastretta-Yanes *et al.* 2015). Among the Mexican mountain ranges, the Sierra Madre del Sur is geomorphologically the most complex, with a marked topography resulting in a mosaic of soils and climatic gradients (Krasilnikov *et al.* 2011). Yet, no gypsum endemic *Pinguicula* species (following the species concept of Lampard *et al.* 2016) was known thus far from the Sierra Madre del Sur before the discovery of *P. pygmaea*—in contrast to the Sierra Madre Oriental of north-eastern Mexico (Coahuila, Nuevo León, Tamaulipas, San Luis Potosí, Hidalgo, to northern Puebla and Querétaro states), likewise a *Pinguicula* diversity center providing various soil types, including gypsum, that host six narrowly endemic gypsicolous species: *P. debbertiana* Speta & Fuchs (1992: 375), *Pinguicula gypsicola* Brandegee (1911: 190), *Pinguicula immaculata* Zamudio & Lux (1992: 40), *Pinguicula nivalis* Luhrs & Lampard (2006: 4), *Pinguicula rotundiflora* Studnička (1985: 201) and *P. takakii* (Zamudio & Lux 1992, Zamudio 2005, Lampard *et al.* 2016).

Taxonomic relationships:—*Pinguicula pygmaea* is closely related to *P. crenatiloba*, a delicate annual species, with which it shares leaves with strongly involute margins (incurved up to 1 mm) in the apical 2/3 of the lamina, calyx shape, and especially the bilabiate corolla with very short and only weakly pronounced tubular throat. However, the former species is readily distinguished from the latter by its corolla, which has subequal lobes with an entire margin and an obtuse to shallowly retuse apex. The corolla lobes of *P. crenatiloba* differ greatly between the upper and lower lip: the lobes of the corolla upper lip are distinctly smaller, more or less rectangular in outline, with bifid apex and acute (rarely obtuse) tips, while the lobes of the corolla lower lip are much larger, with undulate (rarely rotundate) to emarginate apex. In contrast to the strict gypsicolous *P. pygmaea*, the closely related *P. crenatiloba*, and the likewise delicate annual *P. lilacina* (which is of different corolla shape, see Table 1 and Fig. 3) do not occur on gypsum soil, but inhabit clayey soils overlying limestone or igneous rock (Casper 1966, Zamudio 2005).

The delicate habit and the corolla entire lobes and color of *P. pygmaea* are superficially similar to the also annual *P. takakii* (see Table 1 and Fig. 3), which inhabits similar gypsum soils of the Sierra Madre Oriental in San Luis Potosí state, north-eastern Mexico, often sympatric with *P. gypsicola*.

TABLE 1. Comparison of *P. pygmaea*, *P. crenatiloba*, *P. lilacina*, and *P. takakii*. Measurements are taken from examined herbarium specimens and from literature (Ernst 1961, Casper 1966, Zamudio & Rzedowski 1986, Lampard *et al.* 2016).

	<i>P. pygmaea</i>	<i>P. crenatiloba</i>	<i>P. lilacina</i>	<i>P. takakii</i>
leaf	obovate to elliptic, 4–8 × 2.5–5 mm; margins strongly involute	ovate to obovate-oval, 5–14 × 3–7 mm; margins strongly involute	obovate to ovate, 15–55 × 5–30 mm; margins slightly involute	spatulate to ovate, 5–16 × 4–12 mm; margins strongly involute
length of the corolla (including the spur)	(3–)3.5–5 mm	(3–)4.5–6(–7) mm	8–17 mm	6–12 mm
corolla shape	bilabiate, with very short tubular throat that narrows into the spur	deeply bilabiate, generally lacking a pronounced tubular throat	5-merous, cylindrical, tubular throat well expressed and separated from the spur	5-merous, tubular throat well expressed and separated from the spur
corolla lobes	subequal; lobes of corolla upper and lower lip entire, obtuse to shallowly retuse	lobes of corolla upper lip bifid, acute; lobes of lower lip emarginate, undulate, or rarely rotundate	subequal; lobes of both corolla lips entire, obtuse or shallowly retuse	subequal; lobes of both corolla lips entire, obtuse or retuse
habitat	gypsum	limestone, igneous rock, red clay	limestone or igneous rock	gypsum

Other specimens examined (paratypes):—MEXICO. Oaxaca: Município de Tonala: Highway 125, between Huajuapan and Tlacotepec, 1 km south of Tonala, c.1380 m alt., 5 November 2016, F. Rivadavia, R. Resendiz Torreblanca, J.I. Guerrero Argüelles, A. Pérez Ángeles & J. Gomez Landeros 2726 (XAL!); Highway 125, between Huajuapan and Tlacotepec, 3 km south of Tonala, c.1400 m alt., 5 November 2016, F. Rivadavia, R. Resendiz Torreblanca, J.I. Guerrero Argüelles, A. Pérez Ángeles & J. Gomez Landeros 2727 (XAL!); Município de Tlacotepec: on hills next to the Laguna Encantada, c.1680 m alt., 5 November 2016, F. Rivadavia, R. Resendiz Torreblanca, J.I. Guerrero Argüelles, A. Pérez Ángeles & J. Gomez Landeros 2728 (XAL!).

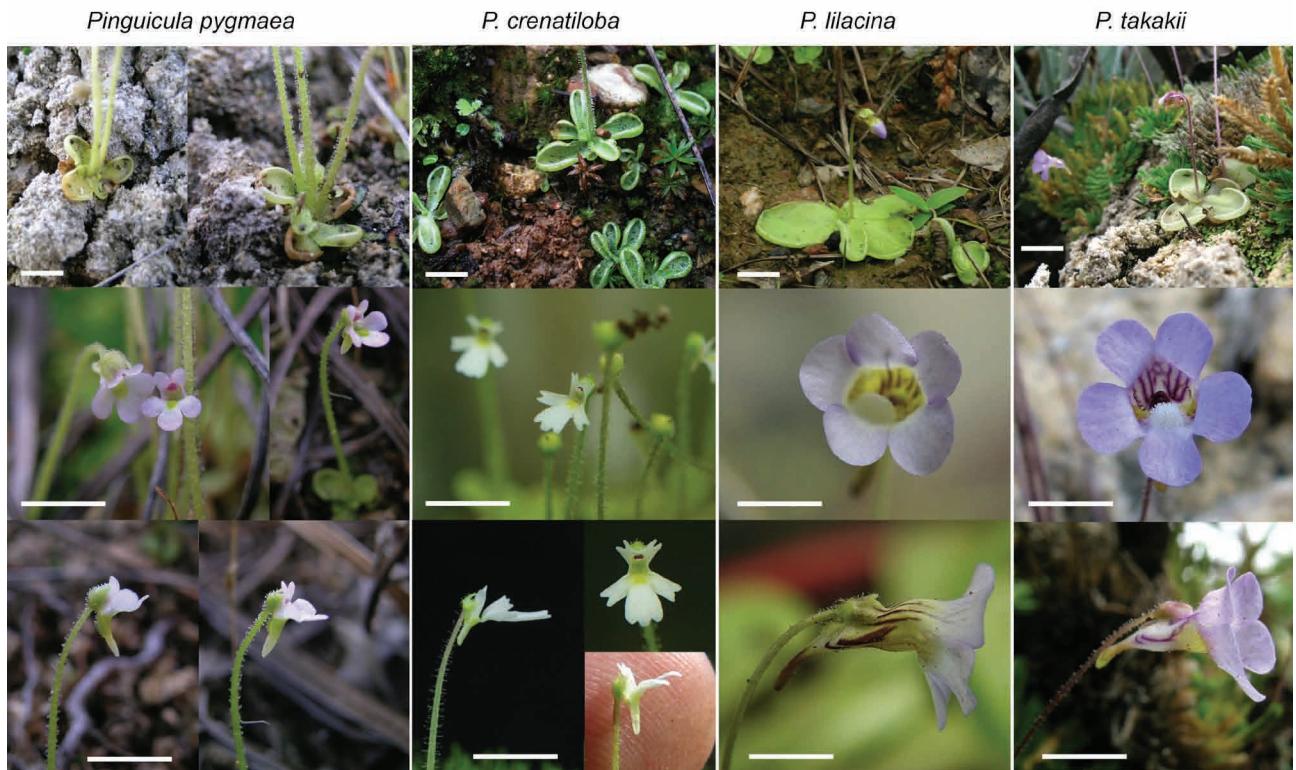


FIGURE 3. Morphological comparison between *Pinguicula pygmaea*, *P. crenatiloba*, *P. lilacina* and *P. takakii*. All scale bars = 5 mm. Photos by F. Rivadavia, except *P. crenatiloba* middle row and lower row right top image, *P. lilacina* middle and lower row (by R. Resendiz Torreblanca) and *P. crenatiloba* lower row left image (by M. Welge).

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APPENDIX 1. Examined specimens of related species (*P. crenatiloba* and *P. lilacina* only considered for southern Mexico).

***P. crenatiloba*:**—MEXICO. **Oaxaca:** Santiago Lachiguiri, Media Loma [c. 800 m], 6 Dezember 1955, *T. MacDougall s.n.* (MEXU 252915!); Santiago Lachiguiri, Tehuantepec, N de Crucero Buenavista [c. 1000 m], 25 January 1992, *V. Alvaro Campos 4293* (MEXU!); Santa María Chimalapa, S de Santa María por la vereda a la Gloria, 350 m, 14 December 1984, *H. Hernández G. 691* (IEB!, MEXU!); San Felipe Usila, senda para la pista de Santiago Tlatepusco, 24 September 1990, *J. Ismael Calzada 16440* (MEXU!); **Guerrero:** Chilpancingo, vicinity of Acahuizotla between Chilpancingo and Acapulco, 17 October 1959, *H. E. Moore Jr. 8122* (MEXU!); W de El Ocotito, camino a Jaleaca, 700 m, 24 November 1983, *E. Martínez S. & F. Barrie 5736* (MEXU!); **Michoacán:** 25 al SW de Arteaga, 900 m, 30 November 1968, *Rzedowski 26636* (MEXU!); **México:** Tejupilco de Hidalgo, puente sobre el Río Chilero, 1700 m, 20 October 1988, *A.R. López Ferraria et al. 792* (IEB!).

***P. lilacina*:**—MEXICO. **Oaxaca:** Santa María Chimalapa, E de Santa María por la vereda a Paso Venado, cerca del entronque don la vereda al Río Piñal, 250 m, 27 October 1984, *H. Hernández G. 536* (IEB!, MEXU!); por la vereda a la cabecera del Río Escolapa, 400 m, 8 February 1986, *H. Hernández G. 2067* (IEB!, MEXU!); cerca de la vereda al Paso de la Cueva del Río del Corte, 250 m, 25 January 1986, *H. Hernández G. 2026* (IEB!); Juchitán, Lázaro Cárdenas, sobre camino a Santa María Chimalapa, 450 m, 1 March 1981, *T. Wendt & A. Villalobos C. 2961* (MEXU!); Santiago Lachiguiri, Tehuantepec, N de Crucero Buenavista, 25 January 1992, *Alvaro Campos V. 4291* (MEXU!); Santiago Lachiguiri, Media Loma, 6 December 1955, *T. MacDougall s.n.* (MEXU 253998!); **Veracruz:** Totutla, Encinal, 750 m, 14 December 1972, *F. Ventura A. 7628* (MEXU!); Xalapa, Tronconal, 1100 m, 28 January 1980, *P. Ventura A. 16783* (MEXU!); Xalapa, hills nearby the Languna del Castillo, 1150 m, 22 December 1989, *M. Chazaro B. et al. 6062* (MEXU!); Xalapa, c. 15 km al SE de Xalapa a camino de Chavarillo, 900 m, 14 February 2016, *F. Rivadavia et al. 2707* (XAL!).

***P. takakii*:**—MEXICO. **San Luis Potosí:** Minas de San Rafael y Guaxcama, 1350 m, 10 November 1965, *F. Takaki 2057* (IEB!); Villa Juárez, Buenavista, 1350 m, 20 Dezember 1980, *S. Zamudio Ruiz 3824* (IEB!); Villa Juaréz, 4 km from Buenavista, c.1420 m, 8 November 2003, *F. Rivadavia, R. Resendiz & A. Ibarra 1806* (MEXU!); Minas de Guascamá, 2 km al SE de Buenavista, municipio de Villa Juárez, 1400 m, 18 November 1989, *S. Zamudio Ruiz 3789* (isotype IEB!).