

PINGUICULA LITHOPHYTICA IS NOT CONSPECIFIC WITH PINGUICULA
JARAGUANA OR A VARIETY OF PINGUICULA JACKII

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Abstract: The taxonomic status of *Pinguicula lithophytica* had been challenged both in publications and in discussions. It was proposed that *P. lithophytica* is conspecific with *Pinguicula jaraguana*. Both taxa represent Cuban endemics but they are from widely separate locations. Comparison with *P. jaraguana* was not considered by Panfet Valdés and Temple as the taxon was unknown to the authors; subsequent awareness did not cause the authors to question their original decision that assigned species status to *P. lithophytica* that some individuals later perceived demonstrated no significant differences to *P. jaraguana*. Recently published and even more recent unpublished information concerning *P. jaraguana* has allowed comparison with previously unpublished information about *P. lithophytica*. Comparison of the morphology of both species, especially of newly described seeds and new or enhanced measurement of leaf length and width and flower characteristics reveals sufficient differences to attest to their being separate taxa. The name *Pinguicula lithophytica* was also presented as synonymous with *P. jackii* var. *parviflora* but this is rejected as the latter name has no valid publication.

Introduction

Since the original descriptions of *Pinguicula albida* C.Wright ex Griseb. and *Pinguicula filifolia* C.Wright ex Griseb. (Grisebach 1866, p. 162), the *Pinguicula* of Cuba received little attention beyond their initial identification until León & Alain (1957) described and keyed all of the then known five species (*P. albida* C.Wright ex Griseb., *P. benedicta* Barnhart, *P. filifolia* C.Wright ex Griseb., *P. jackii* Barnhart, and *P. lignicola* Barnhart). Ernst (1961) revised 35 then globally known taxa within genus *Pinguicula* that then included only five Cuban taxa. This was soon followed by a revision of the genus, then numbering as many as 53 taxa (including natural hybrids and *nomina dubia*), by Casper (1966) still with only five recognised Cuban taxa included. The next review of the now much enlarged genus, with 91 recognised species (excluding sub-taxa) was conducted 50 years later, in two volumes (Lampard *et al.* 2016; Roccia *et al.* 2016), and this recognised nine Cuban taxa. There followed a review of the numerous and mostly recently discovered *Pinguicula* of Cuba (Casper 2019) in which 14 species and one subspecies were recognised, excluding *P. benedicta* that was mentioned as a puzzling “dubious taxon”. Throughout this period, numerous individual papers were published to announce newly discovered species,

notably by Casper but other authors also made contributions. Although the descriptions of new species made some comparisons of related taxa, this was often hampered by the absence of sufficient material, especially observations of living specimens. In addition, key characteristics used for descriptions of new taxa often varied, resulting in an inability to compare characteristics across two or more taxa.

By 2013, the aforementioned two-volume work (Lampard *et al.* 2016; Roccia *et al.* 2016) had begun to attempt to document all known *Pinguicula* taxa (many new species had been discovered since any previous publication describing the genus). As the work progressed, significant disagreement arose with regard to some taxa, in part resulting in *P. lithophytica* being considered conspecific with *P. jaraguana*, as a consequence necessitating that the species description be completed by combining the characteristics of both original taxa. The ongoing absence of an agreement was indicated by inclusion within the description that “future studies may well demonstrate that the separation of the two at subspecies or species rank is merited” (Lampard *et al.* 2016: p. 558, 560). As a result, the identities of the original *P. lithophytica* (Panfet-Valdés & Temple 2008) and *P. jaraguana* (Casper 2003) were blurred, creating a need to confirm or resolve their identities by extending knowledge of their characteristics, especially for *P. jaraguana* that had many morphological features that were entirely unknown or described without accompanying supporting evidence. Later, Casper (2019) declared no reservations with regard to the representation of *P. lithophytica* and *P. jaraguana* as accepted species and criticised their merger, emphasizing his acceptance of the legitimacy of two taxa with his statement:

The ‘mystery’ of the white-flowering ‘*Pinguicula jackii*’ was solved when on 28 Feb 1995, C. Panfet-Valdés, P. Temple and J. Gutiérrez discovered plants that were later described as *P. lithophytica*.

Shortly after publication of the disputed conspecific taxonomic status of *Pinguicula lithophytica* with *P. jaraguana*, Shimai (2017: p. 292) represented the name *P. lithophytica* as synonymous of *P. jackii* Barnhart var. *parviflora* Alf.Ernst. No justification preceded or accompanied the declaration.

Our objective is to clarify the taxonomic status of *Pinguicula lithophytica* by comparing its morphology with the taxa it has been regarded as conspecific with and to clarify its nomenclatural status. To achieve this, we analysed and described the appropriate taxa in detail and considered their nomenclatural history.

Materials and methods

The three species were analysed based on new information and their protologues (Casper 2003; Panfet-Valdés & Temple 2008; and Barnhart 1931). To reduce too great a dependence on published data previously thought to represent *Pinguicula jaraguana* and *P. lithophytica*, measurements were taken from herbarium material of these taxa and used as data for a multivariate analysis. Seven quantitative variables were measured (Table 1) using Motic Image Plus 2.0^{ML} (Motic China Group Co., Ltd.) and the obtained data were tested for a normal distribution using Kolmogorov–Smirnov’s test (KS) (Cox & Small 1978) with Lilliefors’ significance correction (LSC) ($P = 0.000$). Principal Component Analysis (PCA) based on the correlation matrix was carried out by using PAST ver. 3.16 (Hammer *et al.* 2001) in order to reduce the number of quantitative variables and to obtain new axes that better explained the variation of data. The results were plotted in a two-dimensional graph defined by the new axes of the two first principal components (PCs). To standardize the approach, a like-for-like comparison of dried material was used; one leaf per plant was measured, in each case selecting that which appeared average for a particular specimen.

Table 1. Comparisons of selected characteristics of herbarium specimens of *Pinguicula jaraguana* and *P. lithophytica*. Measurements shown as minimum, average and maximum.

Ref.	Characteristic	<i>P. jaraguana</i>	<i>P. lithophytica</i>
LL	Leaf length	(1.00–)1.95(–2.70) cm	(4.30–)6.38(–7.50) cm
LW	Leaf width	(0.40–)0.84(–1.30) cm	(3.50–)4.49(–5.40) cm
CL	Corolla length with spur	(0.90–)1.30(–1.70) cm	(0.80–)1.10(–1.50) cm
ML	Corolla midlobe length	(0.60–)1.02(–1.30) cm	(0.60–)0.85(–1.00) cm
MW	Corolla midlobe width	(0.40–)0.58(–0.70) cm	(0.60–)0.82(–1.00) cm
SL	Spur length	(0.30–)0.46(–0.60) cm	(0.40–)0.53(–0.70) cm
SW	Spur width	(0.20–)0.26(–0.60) cm	(0.20–)0.38(–0.50) cm

All three taxa, *P. jaraguana*, *P. lithophytica*, and *P. jackii*, were studied using field observations (including photographs taken in the field), and from herbarium material (Appendix I). Fresh, mature seeds and capsules were examined and photographed with Canon PowerShot SX70 with Raynox Macroscopic Lens M-150 and Samsung Galaxy S10+ mobile phone. To measure seed dimensions, paper marked with a 1×1 mm. grid was used.

Taxonomic descriptions given by Casper (2019) for the three species were taken as a baseline. The descriptions were amended by applying both the measurements taken from herbarium material and the morphological evidence gained from observations of fresh material.

Descriptions of colours are notoriously difficult to accurately describe and are usually subjective. For example, *Pinguicula benedicta* flowers were first described as “blue” (Shafer 1910; Barnhart in Britton 1920) but, when compared with, *P. jackii* — the only other *Pinguicula* to be described as having a corolla that is blue (though without accompanying evidence) — the *P. benedicta* corolla colour can clearly be seen to be not a true blue, being closer to purple. The colour of any plant feature will vary over its entire surface. Therefore, colour descriptions are our subjective opinion of what best represents any overall surface colour.

The geographical distributions of *Pinguicula jaraguana* and *P. lithophytica* were compared so as to provide non-morphological factors as additional evidence to corroborate or reject earlier proposals of conspecificity. The density of east-Cuban *Pinguicula* species in habitat was arrived at by polygon mapping, using a 6×6 km² grid to calculate the smallest area that includes all mapped locations.

The claimed synonymy of the name *P. lithophytica* with *P. jackii* var. *parviflora* was assessed according to the International Code of Botanical Nomenclature (ICBN, Lanjouw *et al.* 1956) and the International Code of Nomenclature for algae, fungi, and plants (ICN; Turland *et al.* 2018).

Results and discussion

Results from analyses of herbarium material of *Pinguicula jaraguana* and *P. lithophytica* were compared (Table 1) and demonstrate clear differences, in particular when applied to a multivariate analysis (Fig. 1).

Morphological traits measured demonstrated clear differences between the two analysed taxa (Table 1) and PCA indicated two principal components (PCs) comprising 98.92% of total variance for the data (Fig. 1). In general, *Pinguicula jaraguana* has small leaves while those of *P. lithophytica* are larger, with no observed overlap of size ranges for length or width, suggesting these are

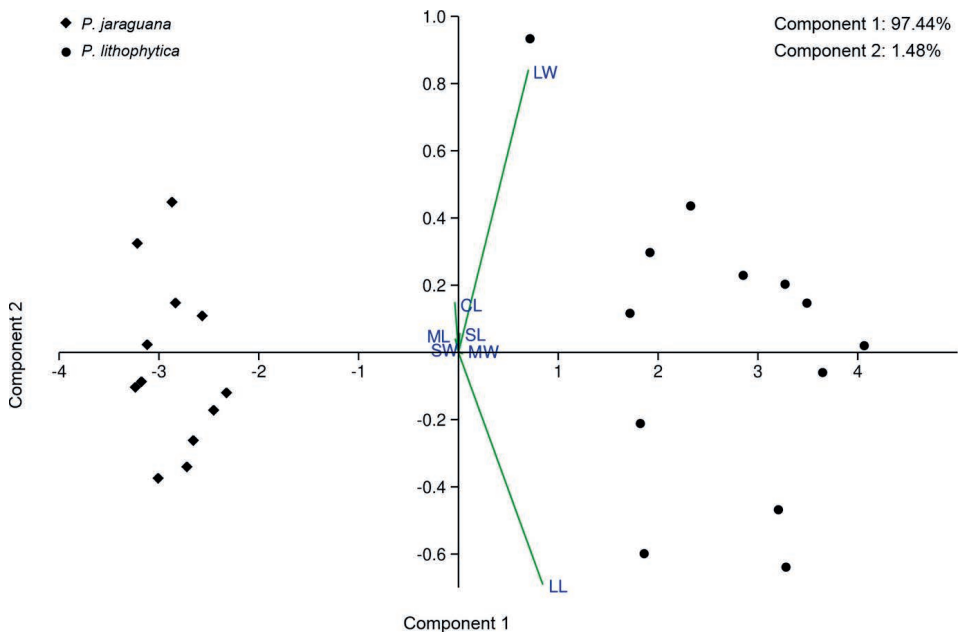


Figure 1: Principal Component Analysis based on selected morphometric characters of *Pinguicula jaraguana* and *P. lithophytica*.

defining characteristics separating the two species as pointed out for the genus by Zamudio Ruiz (2001). The corolla midlobes exhibited significant overlap in size at range extremes but otherwise are different, that of *P. jaraguana* being long and narrow whereas, in *P. lithophytica*, the midlobe is short and wide. The corolla length (without the spur) of *P. jaraguana* is longer than for *P. lithophytica* and this feature also separated the two species based on Component 2 (Fig. 1). This result clearly demonstrates that the multivariate analysis data reflects the presence of two distinct taxa, contradicting any suggestion of the two species being conspecific.

We propose redefinitions for *Pinguicula jaraguana* and *P. lithophytica*., based on those by Casper (2019) but including characteristics that are previously undescribed or which we modify as a result of our observations.

Pinguicula jaraguana Casper (Fig. 2–3, Back Cover)

Perennial herb, scapose, in a basal rosette, (19–)28–42(–60) mm in diameter; lying \pm flat on the ground or somewhat erect, sometimes growing densely grouped together in colonies of many individuals. *Rhizome* short, with fibrous roots. *Leaves* (6–)9–12(–15), yellow-green, succulent, homophyllous, with carnivorous leaves exhibiting seasonally different shape and size (Fig. 3), (10–)19.5–20(–31.6) \times (4–)8–8.4(–13) mm, oblong to spatulate, apex rounded, base narrowly cuneate into a short petiole, margins entire, involute; adaxial surface sparsely covered with glandular trichomes along the veins, the base with many-celled non-glandular trichomes; abaxial surface glabrous. *Scapes* 1(–4), 1-flowered, erect, (70–)110–150(–175) mm long, \pm 0.55–0.60 mm thick, sparsely glandular with \pm 15 stipitate and sessile trichomes/cm². *Flowers* white, indistinctly 2-lipped (subisolobate). *Calyx* yellow-green, distinctly 2-lipped shorter than the tube, \pm 7 mm;



Figure 2: *Pinguicula jaraguana* in habitat.

outer surface sparsely covered with stalked glandular trichomes; upper-lip divided nearly to the base into 3 lobes, lobes oblong-obtuse, apex retuse, $\pm 3 \times 1\text{--}1.5$ mm; lower lip 2-lobed, the lobes free nearly from their bases. *Corolla* (12–)16–19(–22) mm long (including the spur), 22 mm diameter, widely opened, more or less rotate; the lobes recurved, with the tube at an angle of nearly 90° , broadly obovate, margins overlapping for half their length, $9\text{--}12 \times 5\text{--}7$ mm, much longer than the rest of the corolla ($4\text{--}5 \times$ longer than the tube), adaxial surface covered sparsely with non-glandular trichomes that are more abundant at the entrance to the tube; upper lip 2-lobed, lobes smaller than the two lateral lower-lip lobes; lower-lip deeply 3-lobed, lobes obovate, apex rounded, midlobe (6–)9–10.2(–13) \times (4–)5.8–0.6(–7) mm. *Tube* very pale blue-white (almost white), deep purple-blue veins, cylindric, short, (2.5–)3–4(–5) \times 1.5–2.5 mm, without palate; tripartite, the distal part short, narrow, densely covered with long, uniseriate capitate trichomes, the middle part with short multi-seriate capitate trichomes, the proximal part with long uniseriate simple trichomes. *Spur* white, deep purple-blue veins, very short, (3–)4.6(–6) \times (2–)2.6(–6) mm, conical, rounded at the tip, strongly bent forming an acute angle with the tube. *Stamens* ± 1.5 mm long, the short filaments slightly curved; anthers ± 1 mm wide. *Pollen* stephano-4–5-colporate, prolate, surface punctitectate. *Ovary* subglobose-ovoid, sessile, ± 1.5 mm in diameter, 1-loculate, ending in a short style, glabrous. *Stigma* short, 2-lobed, the lower lobe broad, fringed, the upper lobe much smaller, narrowly oblong, fringed. *Capsule* globose, $\pm 3.5 \times 3.5$ mm. *Seeds* dark brown, fusiform, (0.43–)0.50–0.58(–0.65) \times (0.13–)0.15–0.20 mm, testa reticulate, micropylar appendage prominent.

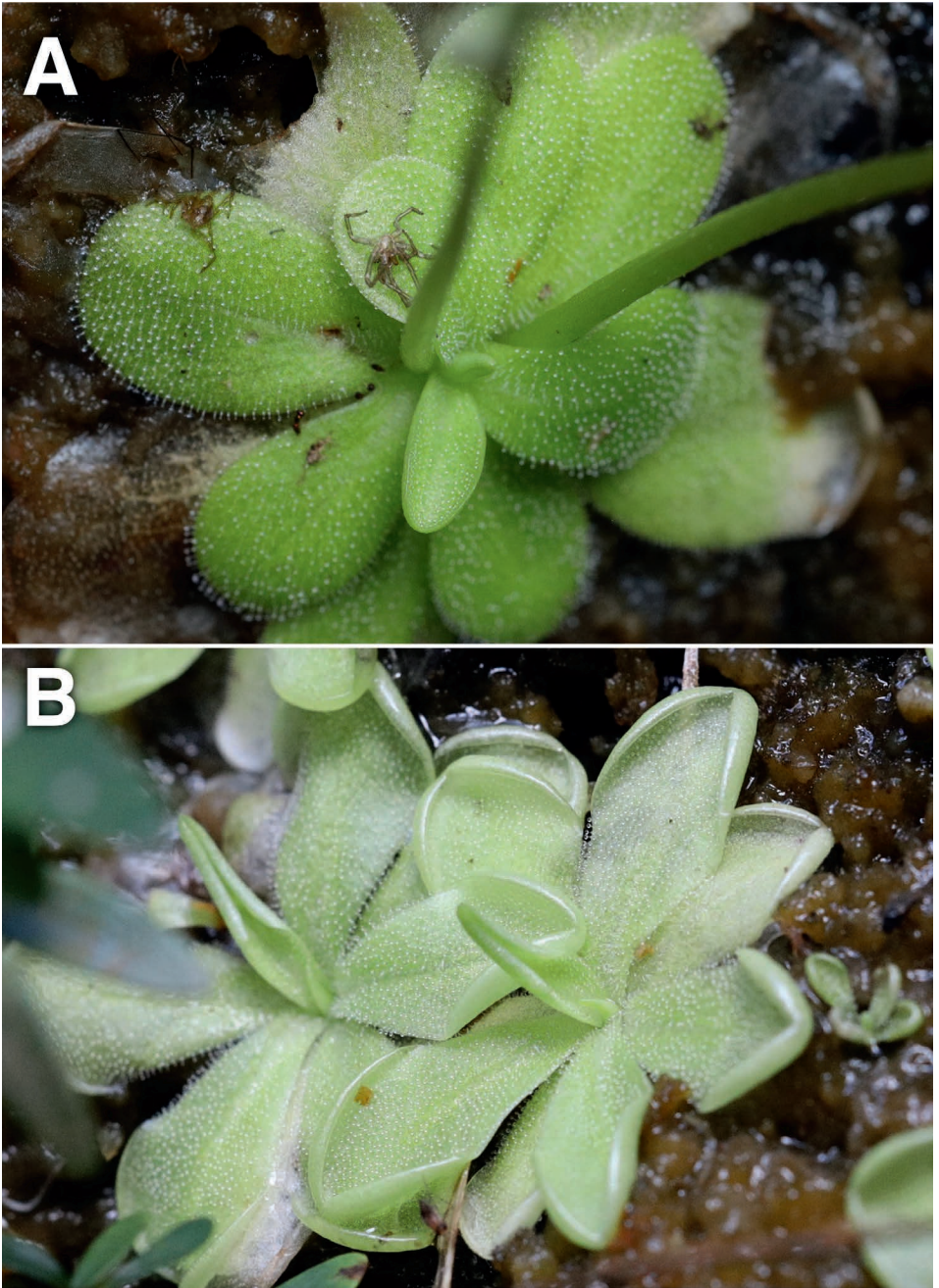


Figure 3: *Pinguicula jaraguana* summer rosette (A) and winter rosettes (B) in habitat.

Pinguicula lithophytica Panfet & P.Temple (Front Cover, Back Cover)

Perennial herb, scapose, in a basal rosette, (80–)100–126(–150) mm in diameter; lying \pm flat on the ground, growing as isolated individuals. *Rhizome* short, with filiform roots. *Leaves* (5–)6–8(–12), green, succulent, homophyllous, with uniform carnivorous leaves all year round, (43–)50–63.8(–75) \times (30–)35–44.9(–54) mm, obovate, apex rounded to obtuse, base cuneate, margins entire, slightly involute; adaxial surface densely covered with sessile and stipitate glandular trichomes, with many glandular trichomes; abaxial surface sparsely covered with stipitate glandular trichomes. *Scapes* 1–3(–5), 1-flowered, erect, (80–)110–150(–180) mm long, \pm 0.80 mm thick, intermediately glandular with \pm 37 stipitate and sessile trichomes/cm². *Flowers* off-white (appearing white), yellow centre, sometimes with faint \pm red-purple lobe margins, indistinctly 2-lipped (subislobate). *Calyx* green, distinctly 2-lipped, shorter than the tube, \pm 5 mm; outer surface covered with stipitate glandular trichomes; upper-lip divided nearly to the base into 3 lobes, lobes oblong, apex obtuse, \pm 2 \times 1–1.5 mm; lower lip 2-lobed, the lobes free nearly from their bases. *Corolla* (13–)14–18(–22) mm long (including the spur), \pm 20–25 mm diameter, widely opened, almost bell-like; the lobes recurved, with the tube at an angle of more than 90°, orbicular to widely obovate, bases overlapping, 7–10 \times 8–10 mm, nearly equally longer than the rest of the corolla, adaxial surface covered with stipitate glandular trichomes at the entrance of the tube; upper-lip 2-lobed, lobes a little smaller than the two lateral lower-lip lobes; lower-lip deeply 3-lobed, lobes nearly orbicular, apex obtuse to rounded, midlobe (6–)7–8(–9) \times (6–)7–9(–10) mm. *Tube* yellow-green, dark yellow-brown veins, cylindric to subcylindric, (3–)4.2–5(–6) \times (2–)3–3.5(–4) mm, without palate; tripartite, the distal part very short, expanded and bell-like, densely covered with long, uniseriate simple trichomes, the middle part densely covered with uniseriate simple trichomes mixed with capitate trichomes, the proximal part densely covered with uniseriate trichomes, mixed with uniseriate capitate trichomes. *Spur* yellow-green, dark yellow-brown veins, medium size, (4–)5.3(–7) \times (2–)3.8(–5) mm, saccate, obtuse. *Stamens* \pm 1.5 mm long, the filaments curved, flattened; anthers \pm 1 mm wide. *Pollen* unknown. *Ovary* ovoid, sessile, \pm 1.0 mm in diameter, 1-loculate, ending in a short style, moderately covered with stipitate glandular trichomes. *Stigma* short, 2-lobed, the lower lobe larger than the upper lobe, crenate. *Capsule* ovoid, \pm 5 \times 4 mm. *Seeds* dark brown, ellipsoid, 0.5 \times 0.45–0.5 mm, testa verrucose, micropylar appendage prominent.

Pinguicula jackii Barnhart (Fig. 4, Back Cover)

Perennial herb, scapose, in a basal rosette, (50–)100–160(–200) mm diameter; lying \pm flat on the ground, growing as isolated individuals. *Rhizome* short, with fibrous roots. *Leaves* (5–)7–10(–14), green, succulent, homophyllous, with uniform carnivorous leaves all year round, (21–)38.5–63.2(–100) \times (17–)26–40(50) mm, obovate to ovate, apex rounded to obtuse, base narrowly cuneate, margin entire, slightly involute; adaxial surface densely covered with sessile glandular trichomes and scattered stipitate glandular trichomes, distinguished by a conspicuous bottle-like stalk cell, with many glandular trichomes; abaxial surface glabrous or with stipitate glandular trichomes sparsely covering the middle vein. *Scapes* 1–2(–5), 1-flowered, erect, (60–)83–108(–170) mm long, \pm 0.80–0.85 mm thick, densely glandular with \pm 58 stipitate and sessile trichomes/cm². *Flowers* purple-blue increasingly diffused with white toward the bases of the lobes, indistinctly 2-lipped (subislobate). *Calyx* green, distinctly 2-lipped, shorter than the tube, \pm 7 mm; outer surface glabrous or sparsely covered with stipitate glandular trichomes; upper-lip divided nearly to the base into 3 lobes, lobes oblong-obtuse, apex obtuse, \pm 2.5 \times 1–1.5 mm; lower-lip 2-lobed, the lobes free nearly from their bases. *Corolla* (22–)27–33(–40) mm long (including the spur), 28 mm diameter, widely opened, almost oblique bell-shaped; the lobes recurved, orbicular to widely obovate, margins not overlap-

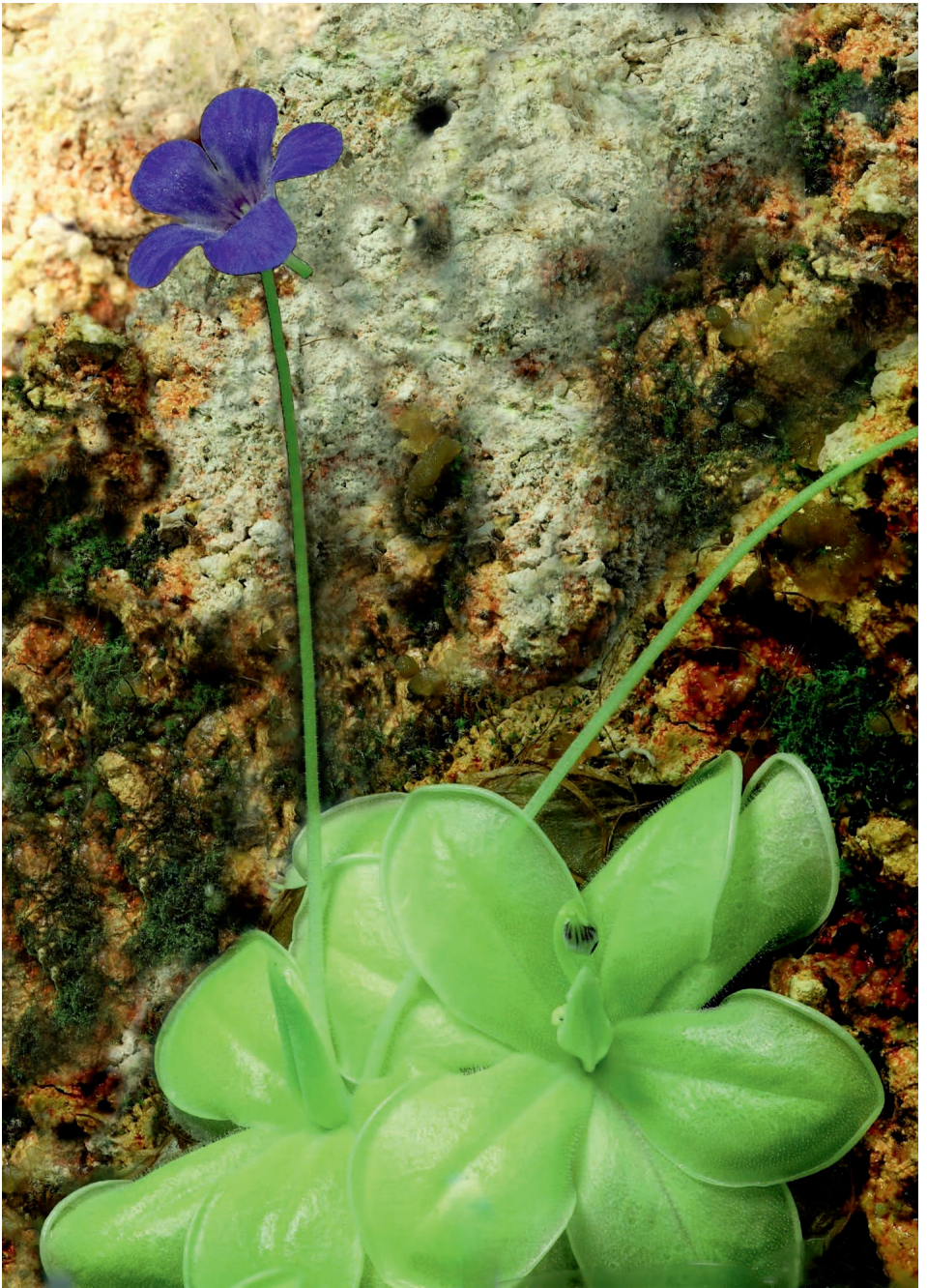


Figure 4: *Pinguicula jackii* in cultivation.

ping, 9–10.3 × 8–10.2 mm, shorter than the rest of the corolla, adaxial surface covered with stipitate glandular trichomes at the entrance of the tube; upper-lip 2-lobed, lobes a little smaller than the two lateral lower-lip lobes; lower-lip 3-lobed, lobes orbicular, apex obtuse to rounded, midlobe (8–)10–10.1(–10.3) × (9–)10.1–10.3(–10.5) mm. *Tube* very pale pink (or purple)-white, grey-purple veins, subcylindric, (8–)10.1–10.3(–10.4) × (8–)10.1–10.3(–10.5) mm, without palate; tripartite, the distal part widely open, densely covered with uniseriate simple trichomes, the middle part densely covered with simple uniseriate trichomes and uniseriate capitate trichomes, the proximal part sparsely covered with uniseriate simple trichome. *Spur* very pale green-beige, indistinct veins, distal end brown-green, 6–10 × 1 mm, slender, rounded at the tip, straight, continuing the tube. *Stamens* ± 1.5 mm long; anthers ± 1 mm wide. *Pollen* stephano-4–5-colporate. *Ovary* globose, sessile, ± 2.5 mm in diameter, 1-loculate, ending in a short style, moderately covered with stipitate glandular trichomes. *Stigma* short, 2-lobed, the lower lobe nearly orbicular, much larger than the upper lobe. *Capsule* globose, ± 5 × 5 mm. *Seeds* dark brown, ellipsoid, (0.32–)0.37–0.45(–0.47) × (0.37–)0.40–0.46(–0.50) mm, testa verrucose, micropylar appendage very short, sunken in a rounded seed end.

The similarly coloured *Pinguicula lithophytica* and *P. jackii* leaves are stronger green (less yellow) than those of *P. jaraguana* leaves. Trichome density varies between the three taxa. The *Pinguicula lithophytica* abaxial leaf surface is entirely and amply covered with trichomes; the emerging involute leaf (Fig. 5) exposes the abaxial surface, clearly revealing that trichomes are not limited either to the edge or to the main vein. While it has not been explicitly stated that trichomes are absent from *P. jaraguana*, no mention of the presence of abaxial leaf trichomes has ever been made, in particular by Casper (2003, 2019). However, we can now confirm that the analysis of fresh material and field observations reveal the absence of trichomes from the abaxial leaf surface of *P. jaraguana*. The presence of trichomes on the abaxial surface of *Pinguicula* is not common and has been reported in just a few species, which suggest it is an important feature in the discrimination of species.

The corolla of the three species is described as subislobate or indistinctly 2-lipped, however, *P. jaraguana* shows a significant imbalance between the upper and lower lips (Fig. 6) while the corolla of *P. lithophytica* and *P. jackii* present an overall appearance of being almost balanced (Fig. 6). Moreover, *P. jaraguana* lobes overlap, from their bases, for between one third to one half of their length. *Pinguicula lithophytica* lobes overlap mainly close to the base or, occasionally, more so, though generally for significantly less than one third of the lobe length and *P. jackii* lobes do not overlap. In addition, the corolla face of *P. jaraguana* is white, deep purple-blue veins occurring



Figure 5: *Pinguicula jaraguana* (A), *P. lithophytica* (B), and *P. jackii* (C) showing emerging involute leaves with no trichomes on abaxial surface, ample abaxial trichomes and sparse trichomes along abaxial midrib, respectively. (Arrows indicate positions of midribs.)

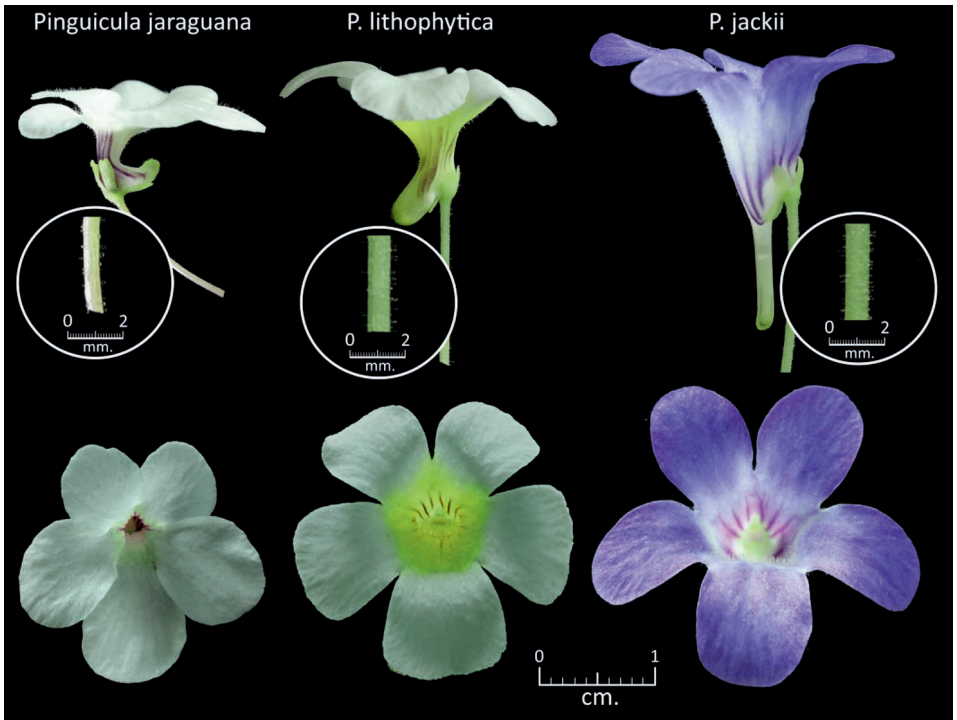


Figure 6: Flowers and scapes of *Pinguicula jaraguana*, *P. lithophytica*, and *P. jackii*.

only within the very pale blue-white (almost white) tube, while *P. lithophytica* shows an off-white (appearing white) corolla face with a yellow centre, sometimes with faint \pm red-purple lobe margins, and dark yellow-brown veins within the yellow-green tube and *P. jackii* shows purple-blue lobes increasingly diffused with white toward their bases, with grey-purple veins within the pale pink (or purple)-white tube (Fig. 6).

During the preparation of *Pinguicula* of Latin America (Lampard *et al.* 2016), a major factor in the decision to merge *Pinguicula lithophytica* with *P. jaraguana* was related to interpretation of the differences in the angles that spurs present to the tubes (i.e., spur-tube angle) that were described as showing considerable intra-specific variation amongst Cuban taxa. A majority of authors held that spur-tube angle was unreliable as a discriminating taxonomic characteristic. This view was over-generalised and thereby misrepresented a significant difference as a result of inappropriately applying data from a sub-set of Cuban species to a wider range of taxa, without supporting evidence. To hold true, the claim of broad intra-specific spur-tube angle variation among all Cuban *Pinguicula* required demonstration. However, at least for some taxa, spur-tube angle can discriminate even at subspecies level, as is true, for example, for *P. filifolia* (Domínguez *et al.* 2014). Further, to merge *Pinguicula lithophytica* with *P. jaraguana*, based (in any part) on the claim that both present significant and overlapping variation in their spur-tube angles, requires evidence specific to this pair of taxa and should not be an assumption that is built upon characteristics evidenced in other taxa. While spur angles can be variable in some species (even to the extent that a single species may exhibit spurs presented at varying angles to the tube ranging between acute and obtuse), our observations and comparisons show *Pinguicula jaraguana*, *P. lithophytica*, and *P. jackii* do not show

such extremes of variation. *Pinguicula jaraguana* consistently presents its spur at an acute angle, *P. lithophytica* shows less spur-tube angle variation but, importantly, the spur is always presented at an obtuse angle. *Pinguicula jackii* bears a spur that consistently presents as a linear extension of the tube (Fig. 6). Thus, spur-tube angles represent a clear, significant, and consistent difference between these taxa.

The scapes of all three taxa show a clear difference in trichome density (Fig. 6). *Pinguicula jaraguana* is described as being only “sparsely” glandular (Casper 2019, p. 74), a subjective description that is open to broadly different interpretations. Comparison reveals that the *P. jaraguana* scape is least glandular, with *P. lithophytica* as intermediate, and *P. jackii* most glandular (Fig. 6), in a density ratio of c. 1:1.2:1.5, respectively. Scape diameter follows the same trend, sizes being c. 0.6 mm, c. 0.82 mm and c. 0.86 mm for *P. jaraguana*, *P. lithophytica* and *P. jackii* respectively.

Pinguicula jaraguana has a capsule that is clearly globose, whereas *P. lithophytica* has a capsule that, though ovoid at first (Fig. 7A) becomes spherical when mature (Fig. 7B). The capsule of *P. jackii* is variable among the specimens observed both in nature and in cultivation.

Representative seeds of *Pinguicula jaraguana*, *P. lithophytica* and *P. jackii* are shown in Fig. 8. Under equal lighting conditions, all three species, were observed to be dark brown, almost black, including both fresh and old seed of *P. jaraguana* and, notably, the seeds of *P. jaraguana* that were not golden, as previously reported by Casper (2019) but pale brown (Fig. 5A). Under normal lighting conditions, *P. lithophytica* and *P. jackii* seeds remained dark blackish-brown but small random areas or patches of golden colour were revealed when seeds were exposed to very bright light (Fig. 5B, C).

Together with the evidence provided by herbarium specimens (Table 1; Fig. 1), ample evidence is presented to demonstrate that the three taxa fully warrant their being considered as non-conspecific. Some of our redescribed characteristics for *Pinguicula jaraguana* reflect our belief that some original data was derived as a result of confusion with another taxon. Casper (2003, 2019) observed only preserved (dried) specimens. Considering *P. jaraguana* is only found in shade habitats (on wet vertical walls,

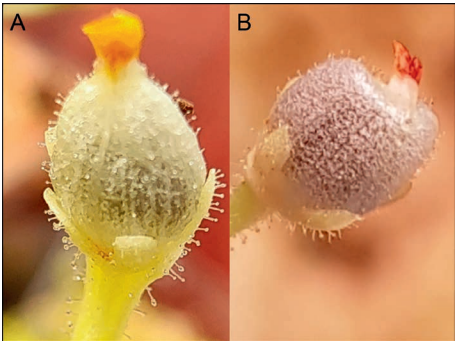


Figure 7: *Pinguicula lithophytica* capsule: immature (A); mature (B).

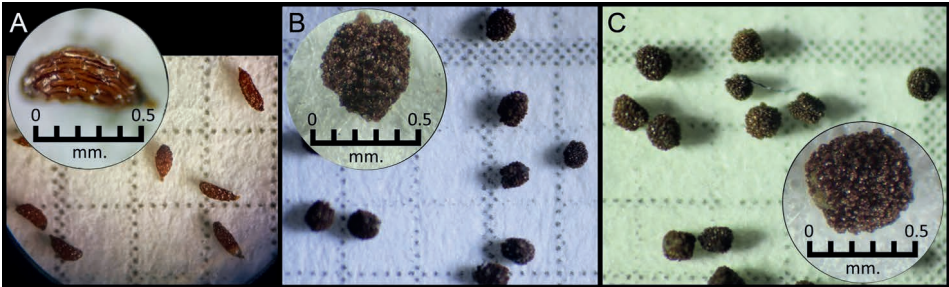


Figure 8: Seeds of *Pinguicula jaraguana* (A), *P. lithophytica* (B), and *P. jackii* (C).

generally associated with a thin layer of *Nostoc* sp. (Nostocaceae), a cyanobacterium, the original description of leaves “in open sun-exposed places often turning red” (Casper 2019) implies that some species other than *P. jaraguana* was being observed, probably *P. benedicta* (syn. *P. caryophyllacea* Casper, *P. toldensis* Casper). Of the remaining characteristics that we redescribe, some were not previously described (or had details omitted). Others apply to characteristics that were based on few specimens; our additional specimens have revealed additional data. In addition, we reject previous measurements of spur diameters that were made using pressed flowers.

Within his recent description of *Pinguicula jaraguana*, Casper (2019) described its capsule and seeds (although unaccompanied by any illustration or photograph):

[*P. jaraguana*] *Capsule* ovoid c. 2 mm long c. 1 mm across, much longer than the persistent calyx. *Seeds* 0.5–0.6 mm long, 0.2–0.3, thick, golden ventrally flat, dorsally convex, testa reticulate, forming a raised network of narrow and sharply angled lines (c. 10) longitudinal rows of right-angled honeycomb interspaces, each depression corresponding an interspace; with single micropylar appendage.

The description of seeds as “ventrally flat, dorsally convex” is contradicted and may be explained by our observations of old herbarium specimens that revealed seeds that appeared excessively dehydrated and damaged, having abnormal or deformed shapes, often with both flat and convex sides. We are aware that Casper only had access to old seeds of *P. jaraguana* from herbarium specimens. Therefore, we believe Casper’s description resulted from his having observed only old, highly desiccated and damaged material that does not accurately represent the shape of fresh seed.

From these descriptions, clear differences can be identified among the three species (Table 2).

As had already been discussed and published (Lampard *et al.* 2016), the distinctly different sub-tropical and humid habitats of *Pinguicula lithophytica* and *P. jaraguana* are limited to the Escambray mountains and Macizo Sagua-Baracoa or Sagua-Baracoa Massif, respectively (Fig. 9). Lampard *et al.* (2016) confusingly described two separate and distinct habitat regions as both belonging to *P. jaraguana* by regarding *P. lithophytica* as conspecific with the former. A brief mention of a biological barrier between the two regions was included but not fully nor accurately described. The Escambray is widely separated from the eastern ranges, the Macizo Sagua-Baracoa and the neighbouring Sierra Maestra — both of which represent sub-tropical cloud forest environments — by the tropical and relatively dry, lowland, Central-East Plain (Planicie Centro-oriental), also but less commonly known as the Camagüey Manaibón (López Almirall *et al.* 1994). The lowland expanse measures c. 250 kilometres long (east-west) and spans the entire area between the north and south coasts. Its impact has long been understood by Cuban botanists but seldom by others. Although the plain does not present a severe impediment to colonisation and spread by plant species, it is a very significant barrier for some, in particular for a group characterised as serpentine flora (López Almirall *et al.* 1994) that includes all terrestrial east-Cuban *Pinguicula*, including *P. jaraguana*.

All the eastern *Pinguicula* species have very limited distributions characterised by serpentine (or ultrabasic) soil — except for the epiphytic *P. lignicola*. Even the modest distances between the various eastern serpentine areas are sufficient to cause isolation of *Pinguicula* populations, such that they become specialised to unique microhabitats, resulting in an unusually high number of species within close proximity, all eight serpentine populations occurring in an area of c. 1350 km², a density of c. 1/169 km² (excluding the epiphytic *P. lignicola*). Compared with gaps between local eastern serpentine habitats, the Planicie Centro-Oriental presents an even stronger barrier as it separates the eastern and central serpentine habitats by a significantly greater distance as well as offering a comparatively drier climate; all east-Cuban *Pinguicula* occur in habitats that are humid combined with

Table 2. Key characteristics of <i>Pinguicula jaraguana</i> , <i>P. lithophytica</i> , and <i>P. jackii</i> .			
	<i>Pinguicula jaraguana</i>	<i>Pinguicula lithophytica</i>	<i>Pinguicula jackii</i>
Rosette diameter	± 40 mm.	± 120 mm.	± 100 mm.
Leaf type	homophyllous, with carnivorous leaves exhibiting seasonally different shape and size.	homophyllous, with uniform carnivorous leaves all year round.	homophyllous, with uniform carnivorous leaves all year round.
Leaf size	± 20 × 8.5 mm.	± 60 × 44 mm.	± 50 × 30 mm.
Leaf abaxial surface	Glabrous.	Whole leaf surface sparsely covered with stipitate glandular trichomes.	Middle vein sparsely covered with stipitate glandular trichomes.
Flower colour	White.	White with yellow throat.	Blue-violet.
Corolla	More or less rotate.	Almost bell-like.	Almost oblique bell-shaped.
Tube	Short, ± 3.5 × 2 mm.	Medium size, ± 4.5 × 3 mm.	Long, ± 10 × 10 mm.
Spur	Very short, ± 4.5 × 2.5 mm.	Medium size, ± 5.5 × 4 mm.	Long, 8 × 1 mm.
Spur-tube angle	Acute.	Obtuse.	Straight.
Capsule	Globose, ± 3.5 × 3.5 mm.	Ovoid, ± 5 × 4 mm.	Globose, ± 5 × 5 mm.
Seed	Fusiform, testa reticulate, micropylar appendage prominent.	Ellipsoid, testa verrucose, micropylar appendage prominent.	Ellipsoid, verrucose, micropylar appendage very short.

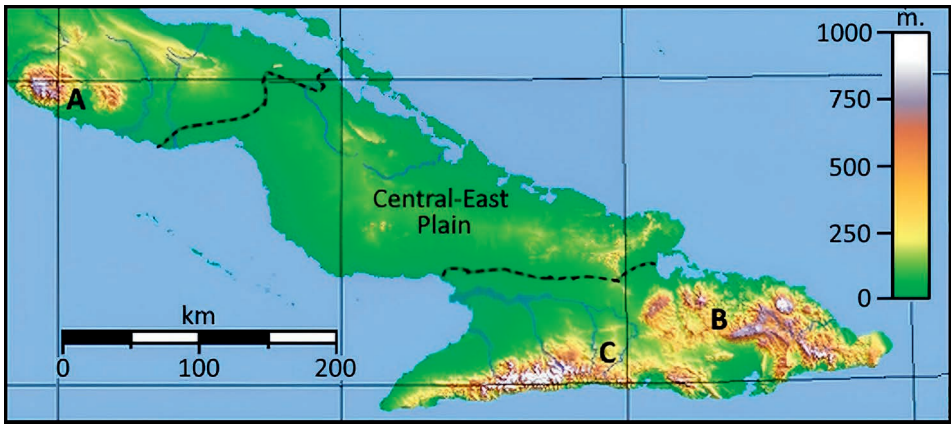


Figure 9: Central and eastern Cuba. The Central-east Plain separating the Escambray mountains (A) in Central Cuba from the Sagua-Baracoa Massif (B) and Sierra Maestra mountain range (C) in Eastern Cuba (map modified from Mapsland.com, 2021).

being seasonally or permanently wet. The plain's temperature is a further constraint; at no point do hills within the Planicie Centro-Oriental rise even to three hundred metres, never coming close to being a mountainous region with an altitude and corresponding lower temperature resembling those in which taxa from the Escambray and Macizo Sagua-Baracoa — including *P. lithophytica* and *P. jaraguana* respectively — live. The Planicie Centro-Oriental experiences typically tropical conditions while the two *Pinguicula* occur at altitudes that are sub-tropical with clouds enveloping the flora at night.

The differences in *Pinguicula lithophytica* and *P. jaraguana* habitats further support their being separate species. *Pinguicula lithophytica* is found on degrading coral-rock seeps, wet during and just after rains but relatively much drier in the absence of recent rain. Plants can withstand long periods of drought, surviving mainly on humidity, even while no rain falls for a month or more. *Pinguicula jaraguana* grows in or by streams, in permanently wet ultra-basic soil.

As previously stated, the name *Pinguicula lithophytica* has also been relegated as a synonymous name of *Pinguicula jackii* var. *parviflora* by Shimai (2017). This was rejected by Casper (2019) with the vaguest explanation: “Ich habe keine entsprechenden Belege gesehen [I haven't seen any corresponding herbarium specimens]”. More specifically, *Pinguicula jackii* var. *parviflora* was first published by Ernst (1961) without designating a type, breaching Art. 40.1 of the International Code of Botanical Nomenclature (ICBN) - Paris Code (Lanjouw *et al.* 1956). A subsequent effort to use Ernst's invalid name was made by Shimai (2017; p. 292) by assigning a neotype but the attempt was not effective as it was contrary to the requirements of Art. 29.1 of the ICN (McNeill *et al.* 2012; Turland *et al.* 2018). No attempt to validate such name is known and since a name has no priority outside the rank at which it is published (Art. 11.2 ICN, Turland *et al.* 2018), even if validated at some point, it would not threaten *P. lithophytica* as the first and hence priority name of the taxon on species rank.

Conclusion

Newly described evidence has reinstated *Pinguicula lithophytica* while *P. jaraguana* is re-described so as to amend and expand details of its characteristics. Using the correct and expanded details, the distinct differences in seed shape, trichome density on scapes, leaf size and the presence, density and distribution of trichomes on abaxial leaf surfaces, and flower characteristics are sufficient to demonstrate that *P. jaraguana* and *P. lithophytica* are distinct species. The invalid publication of “*P. jackii* var. *parviflora*” was not resolved by a subsequent ineffective attempt at typification and that name therefore remains invalid.

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as they affect the plant names discussed above, to Amar Dravid for his precise colloquial translation of Casper's written German, and to Christoph Belanger, for his recommendations on some photography techniques.

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Appendix I — Examined specimens (herbarium acronyms following Index Herbariorum)

- Pinguicula jackii* — CUBA, Cienfuegos: Province of Santa Clara, Las Lagunas, Buenos Aires, about 2500 ft. alt., 5 Dec 1928, *J.G. Jack* 6794 (US!); 7 Mar 1929, *J.G. Jack* 6794 (US!); 25 Apr 1930, *J.G. Jack* 7942 (US!); San Blas, 17 Mar 1929, *L.H. Bailey* 12443 (BH!, NY!); Buenos Aires, Trinidad Mts. 10 Jul 1929, *W.W. Bangham* s.n. (A!); Trinidad Mts, alt. 3000 ft. 12 Mar 1930, *F.W. Hunnewell* 11477 (GH!); Buenos Aires, paredones de los mogotes, 4 May 1932, *J.T. Roig & J. Acuña* 6107 (HAC-Roig!); Lomas de Trinidad, 15 May 1932, *J.T. Roig & J. Acuña* 12916 (HAC-SV!); Vicinity of La Sabana, Buenos Aires, Trinidad Mountains, 5 Aug 1936, *L.B. Smith et al.* 3388 (US!); Trinidad Mountains, San Blas-Buenos Aires, Aug 1941, *R.A. Howard* 6451 (C!, GH!, NY!, Pl, S!, US!); Las Vegas de Mataguá, Trinidad Mountains, 22 Feb 1959, *C.V. Morton* 10527 (US!); Las Villas, Grupo de Trinidad, Kalkfels-Hügel 5 km nw des Topes de Collantes, 800 m, 19 Feb 1968, *Kukan-Dtsch. A. v. Humboldt-Expedition* 1245 (GAT!); La Sierrita, Sabanilla, caminos y farallones en la finca La Cueva, 700–900 msm., 7 May 1977, *J. Bisse et al.* HFC 34920 (HAJB!); Mun. Cumanayagua, Carso de Buenos Aires, Loma Las Lagunas, 21°59'20"N, 80°11'30"W, 750 m., 17 Aug 2014, *B.M. Torke et al.* 1451 (NY!); Province d'Oriente, s.d., s.coll. (MT!); Without information, s.d., s.coll. (HAC-LS!).
- Pinguicula jaraguana* — CUBA, Holguín: Prov. Oriente, Palenque, Cuchillas de Toa, Cayo Fortuna, a lo largo del río Toa, Abr 1970, *J. Bisse* HFC 16747 (HAJB!); *J. Bisse* HFC 16918 (HAJB!); Palenque, Cuchillas del Toa, Cayo Fortuna, Río Toa, después de la entrada del arroyo Cayo Fortuna, 25 Mar 1972, *H. Lippold* HFC 21649 (HAJB!); Mun. Moa, Sierra de Moa, La Melba, Arroyo Jaragua, 25 Feb 1979, *J. Bisse et al.* HFC 39913 (B!, JE!); Palenque, Cuchillas de Toa, Cayo Fortuna, pinares y charrascales en el trillo de Riito a Piloto Arriba, Apr 1972, *R. Berazain & J. Bisse* HFC 21959 (HAJB!, JE!); Moa, Alrededores de la Mina Mercedita cabezadas del río Jiguani, 19 Apr 1985, *A. Álvarez et al.* HFC 56240 (HAJB!, JE!).
- Pinguicula lithophytica* — CUBA, Cienfuegos: Province of Santa Clara, Naranjo, Buenos Aires, Trinidad Hills, 2500–3500 ft. alt., 10 Apr 1930, *J.G. Jack* 7886 (CAS!, SYSU!, US!); Buenos Aires, paredones de los mogotes, 4 May 1932, *J.T. Roig & J. Acuña* 6261 (HAC-Roig!); Trinidad Mountains, limestone hills near El Naranjo, alt. c. 900 m., 18 Jul 1953, *G.L. Webster* 205 (HAC-LS!, MICH!, S!, US!); San Blas, El Sopapo, Los Tornos, 28 Feb 1995, *C. Panfet et al.* HFC 71790 (HAJB!).

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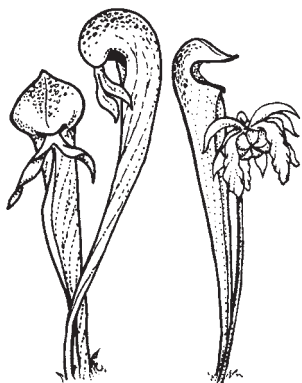
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Front Cover: The Cuban endemic, *Pinguicula lithophytica*, is found only in a small part of the Escambray (or Trinidad) Mountains, where it generally grows on vertical calcareous rock. Photo by Ivan Pančo. Article on page 68.

Back Cover: Flowers of the Cuban endemics, *Pinguicula jackii*, *P. lithophytica*, and *P. jaraguana*, (clockwise from top), showing relative sizes and other characteristics for comparison, in particular their spurs. Composite photo by Ivan Pančo. Article on page 68.

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